BEHAVIORAL CHANGES BY MOHAVE RATTLESNAKES (*CROTALUS SCUTULATUS*) IN RESPONSE TO DROUGHT

A Thesis

Presented to the faculty of the Department of Biological Sciences

California State University, Sacramento

Submitted in partial satisfaction of
the requirements for the degree of

MASTER OF SCIENCE

in

Biological Sciences

(Ecology, Evolution, and Conservation)

by

Michael D. Cardwell

SPRING
2013

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Department of Biological Sciences

Abstract

of

BEHAVIORAL CHANGES BY MOHAVE RATTLESNAKES (*CROTALUS SCUTULATUS*) IN RESPONSE TO DROUGHT

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Michael D. Cardwell

As Earth warms at an unprecedented rate, climatologists warn that droughts will become more frequent and more severe. Previous studies have shown that droughts have already produced profound detrimental effects on reproduction, foraging habits, diet, body condition, and mortality in a wide range of taxa. Yet identifying such effects is often difficult because we know so little about the ecology of so many species. *Crotalus scutulatus*, the Mohave Rattlesnake, is a medically important pit viper that is common in the deserts of the southwestern United States and northern México. Although it produces one of the most toxic venoms of any Nearctic snake and much has been published on its venom and bite, very little is known about its ecology. Pit vipers are underrepresented in the ecological literature, yet have been suggested as good model organisms for studies of the evolution of physiological processes and predator-prey relationships. Given its ecological niche as an ectothermic vertebrate predator in a near waterless environment, in addition to its notoriety as an understudied yet medically significant serpent, *Crotalus scutulatus* is an ideal subject for assessment of survival strategies during drought.

Using radiotelemetry, I collected data during 2224 encounters with 68 male and non-reproductive female *Crotalus scutulatus* between 2002 and 2004 in southern California's Mohave Desert. The area received only 21% of mean annual precipitation in 2002 but returned to 137% and 150% of mean in 2003 and 2004, respectively. The data were examined for behavioral differences between drought and non-drought periods in the context of recent and historical meteorological data, surface topography, floral associations, and sun position.

The study animals relied on preformed body water in their prey as their primary water source. They were apparently obligate surface ambush hunters and remained on the surface to hunt, rather than retreating underground where rodent burrows offered lower thermal maxima and higher humidity that would have slowed evaporative water loss but where foraging success would have been reduced. Cutaneous evaporation represents ca. 75% of total evaporative water loss and is directly related to exposed surface area. The snakes reduced exposed skin by coiling and, when water stressed, by burying their coils in loose soil. They also sheltered behind the raised earthen mounds beneath creosote bushes (*Larrea tridentata*) and moved closer to these shrubs to escape wind and insolation, both of which increase cutaneous evaporation.

______________________________, Committee Chair
Jamie Kneitel, Ph.D.

30 APRIL 13
Date

ACKNOWLEDGEMENTS

So many people and institutions have provided important assistance, support, and encouragement during this journey that I shall certainly omit one or more who are deserving of acknowledgement and I apologize in advance for such omissions.

I thank Jamie Kneitel, my advisor, for his tireless guidance, encouragement, and friendship, as well as for countless epic battles on the racquetball court. I am certainly indebted to my other committee members: Ron Coleman, who introduced me to the intricacies of animal behavior and mathematical modeling techniques, and Winston Lancaster, who provided invaluable guidance and support, including the encouragement to stay at CSUS for graduate school. Jim Baxter's efforts made it possible for me to apply when applications were severely restricted. Bill Avery provided the facility, equipment, and supplies for my analysis of *Crotalus s. scutulatus* diet. Miles Roberts introduced me to geographic information systems (GIS), insured that Geography Department computers remained available, and mentored my GIS efforts throughout these analyses. Jim Alford invested his time and resources to help me interpret vegetation and soil types from satellite images. Tim Horner coached me on the geology of my study area. Nick Ewing expertly assisted with final manuscript preparation.

Bill Hayes and Sean Bush of Loma Linda University provided essential advice and supplies for the 2001–2004 field work and the LLU Animal Research Committee approved my data collection protocol (#82039). Arizona researchers David Hardy Sr. and Gordon Schuett were invaluable mentors. Dale DeNardo, Tracey Brown, Roger

Repp, Emily Taylor, and Matt Goode contributed important suggestions regarding surgery, field techniques, and data processing. Eric Dugan, Chris Rodriquez, and Denise Garland provided frequent assistance with data collection in the field. Cemex Corporation consented to the field work being partially conducted on its property. California Department of Fish and Wildlife granted scientific collecting permits #801125-01, 801165-01 and 801102-04.

Besides producing much of the literature on energy and water flux in desert reptiles, Ken Nagy of the UCLA Department of Ecology and Evolutionary Biology kindly answered my questions as I prepared this thesis. Ken and his former graduate student, Charles Peterson, now of Hofstra University, generously provided hard-to-get publications.

I must acknowledge my parents, Harvey and Bettie, who supported my early interest in wildlife, including my fascination with creatures that others unreasonably fear. More than my early college professors, my wonderful high school biology instructor, David E. Browne, taught me the scientific method and how to search the literature in the old *Biological Abstracts* at UC Riverside, allowing me to pursue my passion informally throughout my three decade detour through law enforcement.

Finally and most importantly, I will be forever indebted to my best friend and wife, Denise. She has been my biggest fan and cheerleader, always encouraging me and never complaining about the enormous amount of time and considerable personal resources devoted to this effort.

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INTRODUCTION

The certainty of a warming planet (Marcott et al. 2013) has focused attention on how climate change is likely to affect habitats and ecosystems the world over. Long-term studies of diverse species strongly suggest that climate change is having a significant effect on populations, communities, and ecosystems worldwide (Parmesan and Yohe 2003). In addition, increasingly severe drought conditions are likely (Solomon et al. 2007) and pose an acute threat to the ability of species to adapt as current climatic zones are pushed toward higher elevations and higher latitudes (Barrows et al. 2010). For example, drought has been associated with changes in foraging habitat and reduced breeding success in Wood Storks (Gaines et al. 2000); changes in diet, lower body mass, and increased mortality in Townsend’s Ground Squirrels (Van Horn et al. 1998); and cessation of reproduction in Blunt-nosed Leopard Lizards (Germano et al. 1994). Sperry and Weatherhead (2008) found reduced body condition and reproduction and increased mortality in Texas Ratsnakes as small mammal populations declined during drought. In one of the only studies addressing the effect of water availability on free-ranging desert rattlesnakes, Schuett et al. (2010) found that drought appeared to be correlated with reduced litter size in Western Diamond-backed Rattlesnakes in the Sonoran Desert.

Deserts are characterized by water being the most biologically limiting resource (Brown and Ernest 2002; Nagy 2004). In addition to being dry, Evenari et al. (1982) described the most common trait of all deserts as the unpredictably of rainfall, with precipitation being highly irregular both quantitatively and spatially. Temperate deserts are also seasonally hot, and variations of weather patterns produce extraordinary extremes of both precipitation and temperature over time. Desert-adapted animals have evolved both physiologically and behaviorally to survive not only the median weather conditions but to persist through the unpredictable yet inevitable extremes.

Understanding these evolutionary adaptations is key to understanding how animals survive in these harsh environments, as well as anticipating how organisms may be affected as our planet continues to warm at an unprecedented rate (Sterl et al. 2008). Yet, as Parmesan et al. (2000) observed, the specific causes of various species' response to climate change are often elusive because we know so little about the natural history of so many taxa.

PIT VIPERS AS MODEL ORGANISMS

Pit vipers (Viperidae: Crotalinae) are venomous snakes with long folding maxillary fangs and infrared-sensing receptors in the face. They are well represented in the deserts of the southwestern United States and northern México by the rattlesnakes (genera *Crotalus* and *Sistrurus*). Pit vipers are underrepresented in the ecological literature yet have been suggested as good model organisms for investigations concerning the evolution of physiological processes, reproductive systems, and predator-prey relationships (Duvall et al. 1992; Schuett et al. 2002; Nowak et al. 2008).

Rattlesnakes are ambush predators of small vertebrates. Adults of all but the smaller species consume large numbers of rodents (Campbell and Lamar 2004), many of which damage human property and act as disease vectors for plague and Hantavirus.

Rattlesnakes use their venom to chemically mark (Chiszar et al. 1983; Saviola et al. 2012) and incapacitate bitten prey animals (reviewed in Mackessy 2008). Snake venoms are known to be complex cocktails of up to a hundred enzymes and other proteins that vary between species, as well as geographically and ontogenetically within species (Glenn and Straight 1978; Mackessy 2010). This variation in venom components is hypothesized to correlate with diet (Daltry et al. 1996) and potentially with foraging strategy (Mackessy 2008).

Finally, snake venoms are among the most complex toxins in the natural world, creating challenges for clinicians treating snakebite patients, yet providing fertile ground for development of new therapeutic drugs for humans (Fry et al. 2006; Mackessy 2010). Clues to potential therapeutic uses of venom components hinge not only on our knowledge of the molecular constituents of venoms, but also on our understanding of how venoms are employed in nature and their evolved physiological effects on prey.

CROTALUS SCUTULATUS

Crotalus scutulatus scutulatus, the Northern Mohave Rattlesnake, is often referred to as simply the Mohave (or Mojave) Rattlesnake, *Crotalus scutulatus*, and is distinct from the other recognized subspecies found in the Méxican state of San Luis Potosí: *Crotalus scutulatus salvini* (Campbell and Lamar 2004; Crother et al. 2012). *Crotalus s. scutulatus* is a commonly-occurring animal on the bajadas and basins dominated by *Larrea tridentata* (Zygophyllaceae; creosote bush) in the Mohave, Sonoran, and Chihuahuan Deserts (Klauber 1972; Campbell and Lamar 2004; Fig. 1) and is frequently

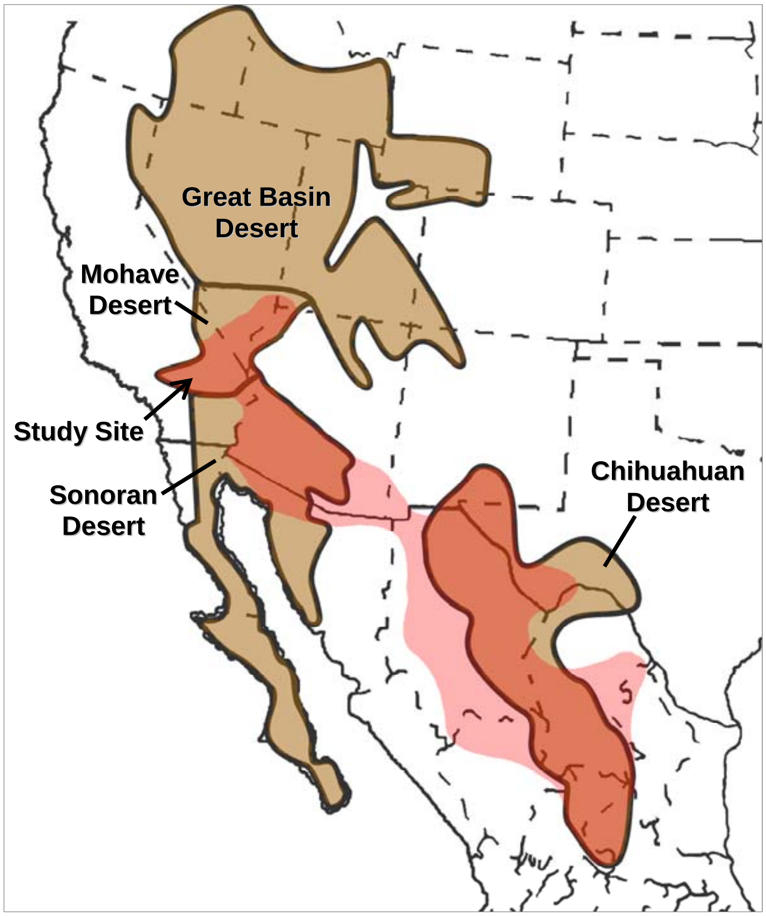

Figure 1. Map of the southwestern United States and northern México showing the distribution of *Crotalus scutulatus* (orange shaded area) in relation to the four major North American deserts and my California study site in the southwestern Mohave Desert at 34^{o} 36′ N 117^{o} 10′ W.

cited as being the most dangerous of all the rattlesnakes (e.g., Schoenherr 1992; Ivanyi 2000; Ernst and Ernst 2012). The venom of *C. s. scutulatus* is well known for its geographic variation (Glenn et al. 1983; Massey et al. 2012), with most populations producing venoms with smaller LD_{50} scores (the dose that kills 50% of lab mice; lower score = greater lethality) than other North American snakes (Minton 1959; Russell 1980; Glenn and Straight 1982). The notoriety of the species' highly toxic venom has spawned a rich folklore (MDC unpublished data) concerning the origin of *C. s. scutulatus*, its alleged distribution, aggressiveness, hybridization, bite effects, and other aspects of its biology and medical significance (e.g., Dibsie 2000; Staff Reports 2008; Jaslow 2012).

Despite many *in vitro* studies of its venom and investigations of its reproductive biology via examination of museum specimens (Goldberg and Rosen 2000) and assays of circulating sex steroids (Schuett et al. 2002), little was known about the natural ecology of *C. s. scutulatus* before my 2001–2004 field work (Cardwell 2006, 2008).

THE MOHAVE DESERT

The Mohave Desert occupies almost all of southern Nevada, that portion of California east of the southern end of the Sierra Nevada Mountains and north of the Transverse Ranges, and small adjacent areas of southwestern Utah and northwestern Arizona. It is bordered by the higher and colder Great Basin Desert to the northeast and by the lower and warmer Sonoran Desert to the south and southeast. Most of the annual precipitation in the Mohave Desert, particularly in the western portion, is provided by cold winter storms. Summer thunderstorms are neither as frequent nor as dependable as the monsoons that routinely drench the Sonoran and Chihuahuan Deserts during the summer (Jaeger 1957; Hulett and Charles 1999; Schuett et al. 2010).

Pavlik (2008) described California’s deserts as a conspiracy of extremes. Air temperatures vary wildly in both winter and summer. Due to the highly porous alluvial soils that make up the basins and bajadas, surface water is virtually nonexistent during the summer, except for brief periods of ephemeral runoff during the occasional thunderstorms. During the summer, the desert air is so dry that any residual moisture quickly evaporates from soil, leaves, and lungs (Pavlik 2008).

The Mohave Desert is dominated floristically by the ubiquitous perennials *Larrea tridentata* and *Ambrosia dumosa* (Asteraceae; burrow-weed), in addition to many other halophilic taxa that are less abundant (Baldwin et al. 2002; MacKay 2003). In response to seasonal rains in both winter and summer, a wide variety of annual plants germinate, mature quickly, and produce seed before desiccating in the heat. The geographic distribution of *Yucca brevifolia* (Lilliaceae; Joshua tree) is virtually synonymous with the boundary of the Mohave Desert (Jaeger 1957; Schoenherr 1992; Baldwin et al. 2002).

WATER FLUX IN DESERT RATTLESNAKES

Terrestrial animals, both desert and non-desert, are composed of 65–75% water (Nagy 2004). Daily water flux, however, varies greatly based upon such factors as endothermy verses ectothermy, habitat aridity, season, and diet. According to Nagy (2004), desert reptiles, in particular, reduce their water flux primarily through physiological and behavioral adaptations, rather than through reduced metabolic rates, compared to taxa from more mesic habitats.

Desert rattlesnakes use extrinsic energy to regulate body temperature (ectothermy) and a sit-and-wait foraging strategy. As ambush foragers, they can rely on anaerobic metabolism for brief periods of activity, rather than on more aerobic metabolism (and, thus, higher resting metabolism) as active foragers require. The combination of a primarily sedentary life style, ectothermy, and reliance on anaerobic metabolism makes desert rattlesnakes some of the best examples of low energy systems among the terrestrial vertebrates (Pough 1980). Field studies on the metabolism of other desert rattlesnakes using double-labeled water confirm their extraordinarily low energy requirements (e.g., Secor and Nagy 1994; Beaupre 1996).

Cohen (1975) experimentally investigated water loss in *Crotalus cerastes* (Sidewinder), a desert rattlesnake that is sympatric over a wide area with *C. s. scutulatus*, and found that cutaneous evaporation was responsible for ca. 75% of evaporative water loss while pulmonary evaporation accounted for ca. 25%. He concluded that evaporative water loss was primarily a function of exposed surface area and was strongly influenced by temperature and air flow. He found that evaporative water loss in snakes that were allowed to coil was significantly less than in uncoiled snakes and he hypothesized that snakes could reduce their evaporative water loss by behavior that reduces exposed surface area and exposure to moving air. The latter is important because it disturbs the boundary layer of moist air against the skin.

Dmi’el (1985) made similar observations of the non-venomous desert snake *Spalerosophis diadema* (Colubridae) from the Sinai Peninsula, finding that cutaneous evaporation accounted for 70–73% of total evaporative water loss and was significantly influenced by air temperature, wind velocity, and body size and shape. He determined that cutaneous evaporation per unit of body surface area is independent of body mass. Following a later study of several Middle Eastern species of Viperidae (Dmi’el 1998), he concluded that interspecific variation in evaporative water loss is better correlated with environmental factors than with phylogenetic relationships.

ASSUMPTIONS AND HYPOTHESES TO BE TESTED

While designing tests for my hypotheses, I made three assumptions about *C. s. scutulatus.* First, I assumed that their prey was their principal water source. Furthermore, during hot weather, I assumed that rodent burrows offered refugia with higher humidity and lower thermal maxima which would reduce evaporative water loss compared to surface conditions. Finally, I assumed that water replacement depended upon eating and that these rattlesnakes are obligatory surface ambushers. I tested the hypotheses that, in proportion to their degree of water stress, the rattlesnakes reduced evaporative water loss by selecting ambush locations with slope and aspect that minimized exposure to solar heat, reduced their wind exposure, and used “cratering” (partial burying of their coiled bodies in loose soil) to reduce skin area exposed to hot dry fluid air.

METHODS

STUDY SITE LOCATION AND CLIMATE

Data were collected in the western Mojave Desert near Victorville, San Bernardino County, California, USA, at 34^{o}36´N, 117^{o}10´W (NAD83). The study site was dominated by creosote bush (*Larrea tridentata*) and covered ca. 150 ha at the confluence of two bajadas demarcated by an ephemeral wash. Median elevation was ca. 975 m. (Figs. 2, 3)

There was little variance in mean monthly temperature or relative humidity between 2002, 2003, and 2004 (National Climatic Data Center 2001–2004; Western Regional Climatic Center 2010; Fig. 4). However, annual precipitation (measured at NOAA Station 049325/99999, 14 km SW of my study site) varied greatly, with 97% of the 30-year mean (15.8 cm) in 2001, 21% in 2002, 137% in 2003, and 150% in 2004 (National Climatic Data Center 2002a, 2001–2004; Fig. 5).

While precipitation data from nearby recording stations proved to be valuable indicators of the general conditions at my study site, particularly regarding cold winter storms, they were less valuable for measuring rain from warm summer storms (MDC pers. obs). Winter storms blew in over the Transverse Ranges from the Pacific Ocean and were often large generalized weather events of relatively long duration. Summer thunderstorms, however, came from the south, forming individual cumulonimbus cells that produced localized linear rainfall patterns as they blew across the desert. Although

Figure 2. Typical creosote bush scrub bajada habitat near the center of my study site.

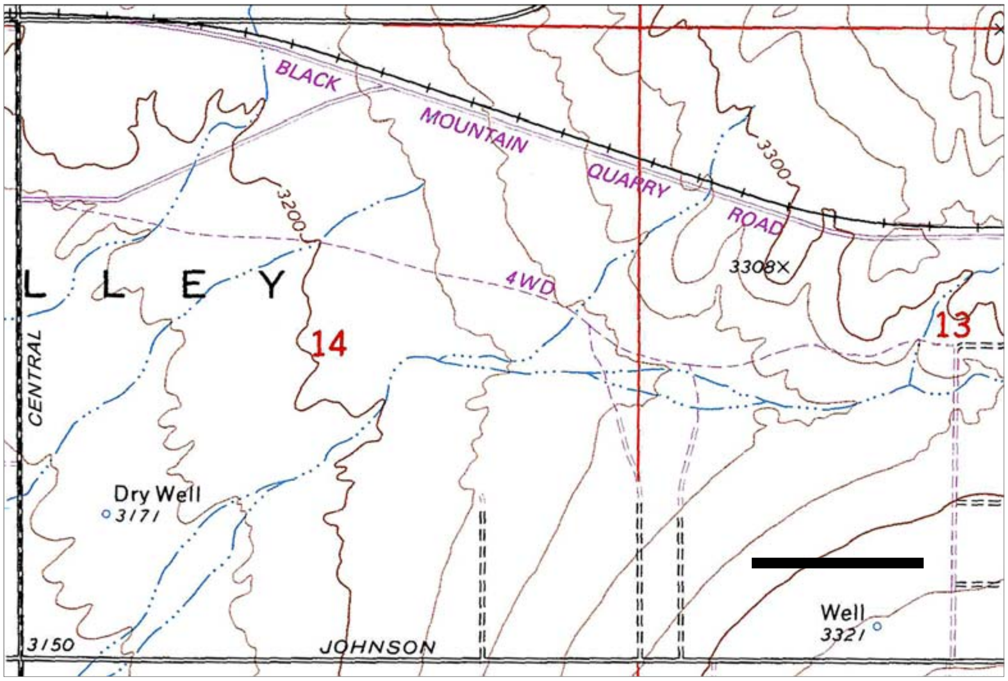

Figure 3. Topographic map of my study site enlarged from USGS 7.5´ Apple Valley North quadrangle. Central Road is grid north/south. Elevation units = feet; contour interval = 20 ft (6.1 m); broken blue lines = major ephemeral washes; bar = 500 m. Source: United States Geological Survey.

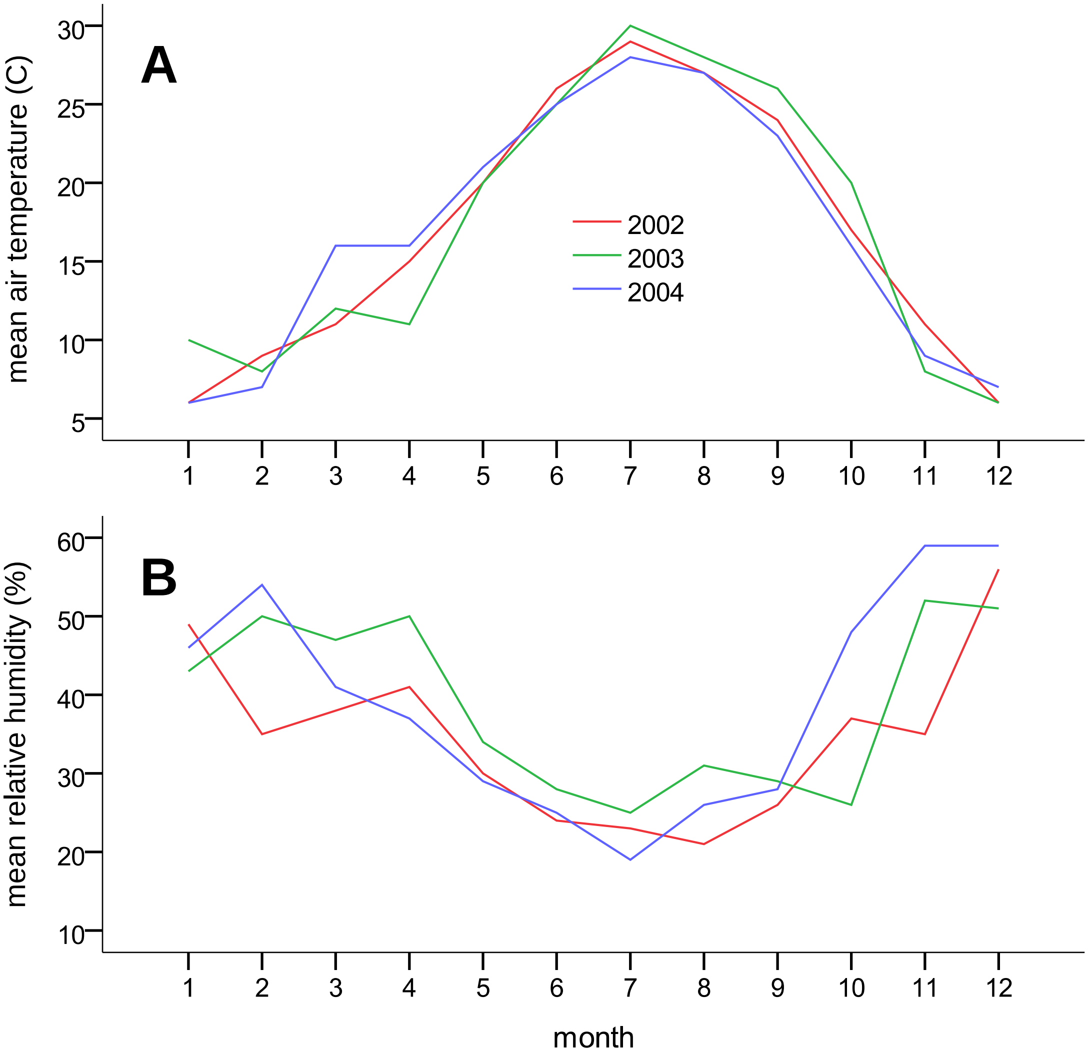

Figure 4. Mean monthly air temperature (**A**) and mean monthly relative humidity (**B**) for 2002, 2003, and 2004, computed from data recorded at El Mirage, 35 km WNW of my study site (Source: Western Regional Climate Center, Desert Research Institute, Reno, Nevada). Months 1–12 = January–December.

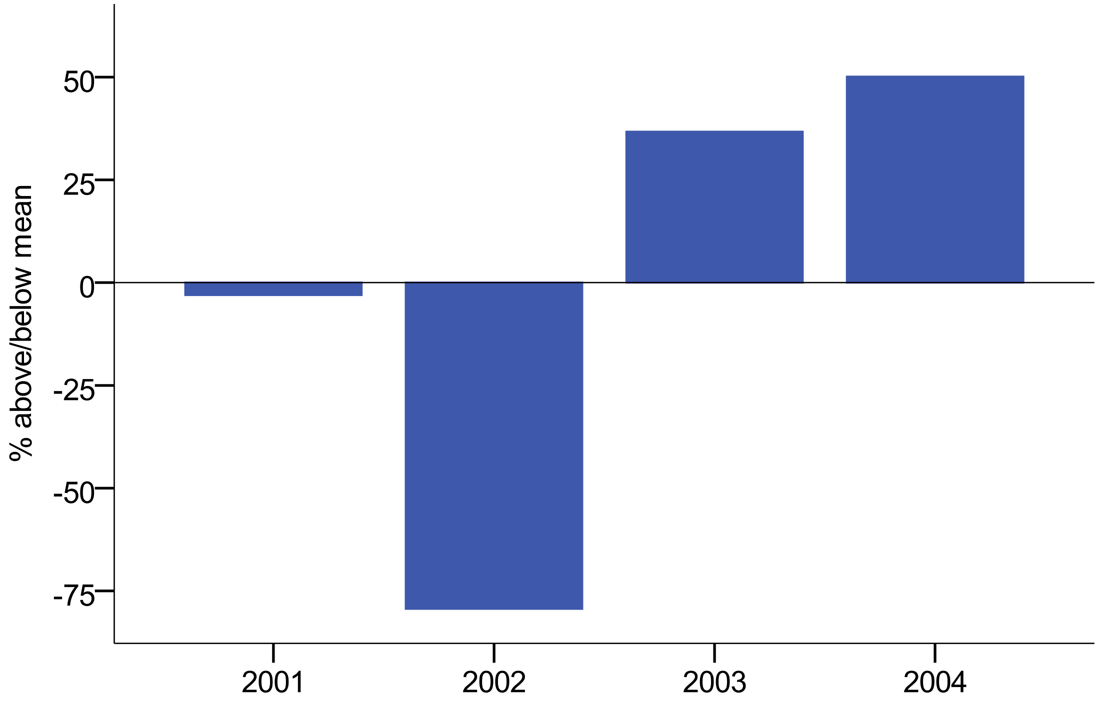

Figure 5. Annual precipitation above and below mean, computed from data recorded at Victorville, 14 km SW of the study site. Thirty-year (1971–2000) mean = 15.8 cm. (Source: NOAA Annual Climatological Summaries for Station 049325/99999)

they frequently delivered heavy downpours, these storms were sometimes no more than a kilometer wide, with demarcated margins and dry desert just a few meters beyond. Thus, any particular storm left the vast majority of the region dry. Even for a location in such a storm's path, the rainfall duration was often no more than a few minutes.

Because of the random and localized nature of summer rainfall in the area, it was necessary to rely on my personal observations to assess the desiccation of my study site during 2002. Only two brief showers, producing superficial moisture that rapidly evaporated (24 April and 10 July), occurred at my study site during 2002 before the drought was ended by substantial Pacific storms that began arriving on 9 November 2002. Despite the U.S. Weather Service reporting that a "wetter than normal September" had interrupted the extreme drought in the southwestern United States in 2002 (National Climatic Data Center 2002b), my recent tracks were only pockmarked by raindrops on 1 and 4 September.

RADIOTELEMETRY

Due to the paucity of natural history information for *C. s. scutulatus*, my initial objective was to collect as much observational data as possible on the behavior and habits of free-ranging *C. s. scutulatus.* To that end, I attempted to maintain seven telemetered adult *C. s. scutulatus* of each sex. When a telemetered animal was lost, it was replaced by the next suitable animal encountered. The first transmitter was implanted in male Css02 on 23 August 2001, and the last new animal, male Css64, was implanted on 28 March 2004. Routine data collection was discontinued on 22 November 2004, when a blanket of snow ensured the end of the activity season.

In total, 10 male and 10 female *C. s. scutulatus* were surgically implanted (Hardy and Greene, 1999, 2000; Reinert, 1992; Reinert and Cundall, 1982) with 9 g temperature-sensing radio transmitters (model SI-2T by Holohil Ltd., Ontario, Canada) and radio-tracked for periods ranging from 9 to 1015 d (mean = 570 ±362 SD). Transmitters did not exceed 5% of body mass (Reinert 1992).

With few exceptions, all telemetered animals were located and documented at least once during each field day. Excluding one absence of fifteen days in July 2004, the mean interval between field days (calendar dates) during the combined activity seasons (excluding winter months) was 1.1 d (±1.4 SD, range 0–8, n = 459). Field effort was generally timed to coincide with environmental temperatures favorable for activity, although some visits were intentionally carried out during thermal extremes.

ANIMAL PROCESSING

All non-telemetered rattlesnakes encountered (both new and recaptures) were removed from the field for processing, except animals that were *in copulo* and those that had been processed within the previous few months. Telemetered animals were processed annually during transmitter replacement. All animals, including post-surgical subjects, were released as soon as possible at their capture locations, often within 24 h.

In addition to standardized data (see below and Appendix A for details), processing after capture included determination of mass (to ± 0.5 g; Ohaus decigram balance), precise snout-vent and tail length (under general anesthesia), verification of sex by probing (Schaefer 1934), rattle condition and dimensions, identification photos, and colored marking of penultimate rattle segments for quick visual identification. All animals captured after 2001, except late-term pregnant females, were implanted with a passive integrated transponder (PIT) tag (Avid Identification Systems, Norco, CA, USA) in the posterior coelom.

STANDARDIZED DATA

Standardized data (a standardized list of observations and measurements; see Appendix A) were recorded at each encounter, using Pendragon® Forms v.3.2 (Pendragon Software, Libertyville, Illinois, USA) on a hand-held Palm® IIIc Personal Data Assistant (Palm Computing, Santa Clara, California, USA), and later transferred to Excel® v.2002 (Microsoft Corp., Redmond, Washington, USA) spreadsheets.

Geographic locations were determined with handheld Global Positioning System (GPS) receivers. Prior to April 2003, a Garmin® 12XL GPS receiver (Garmin International Inc., Olathe, Kansas, USA) yielded indicated errors between 2.7 and 6.7 m (mean = 3.7). Beginning 2 April 2003, a Garmin® 72 GPS receiver was used in "WAAS enabled" mode, consistently yielding < 3.0 m error.

Photoperiod was recorded as "day," "night" or "twilight" based on sunrise and sunset times, as well as the duration of "nautical twilight," as determined for each date from the United States Naval Observatory website (http://www.usno.navy.mil/).

Air temperature at each encounter was measured in sun and shade with a quick-reading Hg cloacal thermometer (Miller and Weber, Inc., Ridgewood, New York, USA) about 1 cm above the substrate and recorded to the nearest 0.5^{o} C.

Wind velocity was measured for ≥15 s with a Kestrel 1000® hand-held anemometer, set to “average” mode, and rounded to the nearest 5 km h^{-1}. Wind direction was estimated to the nearest 22.5° (i.e., N, NNE, NE, ENE, E) relative to grid north.

Core body temperature was calculated to the nearest 1° C for each observation by timing transmitter pulse intervals three times with a stopwatch, then comparing the mean to a chart supplied by the transmitter manufacturer. Prior to implantation, each transmitter was tested in an H_2O bath at room temperature and the result was compared to the manufacturer’s chart. The pulse interval-to-temperature conversion charts supplied by the manufacturer were found to yield values up to 1.5° C greater than my measured H_2O bath results, resulting in body temperatures calculated from some transmitters being reduced accordingly.

“Overhead Environment” referred to the area directly above a snake: “clear” indicated unobstructed sky, “foliage” indicated that the subject was under the branches of a perennial shrub, “in burrow” was used when an animal was inside a subterranean burrow, and “debris” was used when a snake was under man-made material. When a snake’s body extended from one overhead environment to another, the location of the snake’s head was used.

See Appendix A for more details of standardized data fields and definitions.

METEOROLOGICAL DATA

Historical precipitation data were obtained from the National Oceanic and Atmospheric Administration for its “Victorville Pump Plant” station (COOP ID

049325), located 14 km southwest of the study area (National Climatic Data Center 2001-2004, 2002a). Recent daily temperature and humidity data, recorded 35 km west of my study site in similar contiguous habitat at El Mirage, were obtained from the Western Regional Climatic Center (2010). I also measured air temperatures at each encounter with a study animal (see Serial Data, above).

GEOGRAPHIC INFORMATION

I used ArcGIS 9.3.1 software (ESRI, Redlands, California, USA) to build a GIS (Geographic Information System) database of my study site. A satellite photograph of the study area purchased in 2005 from TerraServer (Raleigh, North Carolina, USA) was used as the primary reference layer. This raster image was rectified to remove distortions by modifying it to match the San Bernardino County street centerline file <countywide_ centerlines_02_28_2011.zip> (downloaded 7 March 2011from ftp://gis1.sbcounty.gov/). The image was then saved in .TIFF format and used to create the first shape file in the GIS database. The new shape file was assigned the same geographic referencing system as the centerline file on which it was based: NAD_83_StatePlane_California_V_FIPS_ 0405_ Feet. This and all subsequent shape files were assigned this geographic reference system and converted to North American map datum 1983 (NAD83).

Elevation data were obtained in the form of 1:24000-scale United States Geological Survey (USGS) digital elevation model (DEM) files. USGS makes these data files available to the public via agreements with private companies, such as MapMart (www.mapmart.com), where I downloaded the file <3990284.DEM. SDTS.TAR> on 10 March 2011. I used "7zip" (version 4.57, downloaded 10 March 2011 from www.izarc.org) to extract the digital elevation model files from the Tape Archive (TAR) file. I used ArcGIS 9.3.1 to produce an elevation shape file with a 5 m contour interval directly from the un-zipped digital elevation model files. The metadata accompanying the digital elevation model files indicated that the aspect values were relative to magnetic north and listed the XY resolution as 10 m and the Z (vertical) resolution as 0.1 m. I used ArcMAP (a subset of ArcGIS) to generate slope and aspect data sets directly from the digital elevation model files. These data were used to create separate slope and aspect map layers. For analysis with my 2001–2004 data, I subtracted the declination of 13^o (indicated on USGS Apple Valley North 7.5′ quadrangle map) from the magnetic aspect values to yield true north values. I made no distinction between true north and grid north throughout these analyses because the difference was only 0^o 6´, per the USGS Apple Valley North 7.5´ topographic map.

"General soil map units" at the study site and an associated geospatial map (soil_ca671.zip) were obtained from the United States Department of Agriculture (1986). These data yielded a georeferenced GIS soil map layer that proved to be very accurate when I later ground-truthed these data with the Garmin® 72 GPS receiver.

Additional soil information was obtained from the TerraServer satellite photograph and a visit to the site on 22–23 March 2011. Patches of ground covered with small angular stones with the clay and metal oxide coating known as "desert varnish" were found to be mostly within the USDA soil survey map unit identified as "Mirage sandy loam" but the rocky patches did not cover the entire map unit. These rock-strewn areas appeared as dark reddish-brown areas on the satellite image and their margins were digitized on the rectified GIS soil layer.

MODELING EVAPORATIVE WATER LOSS

I used previously published data to construct a mathematical model of the progression of dehydration due to evaporative water loss in *C. s. scutulatus* during the summer of 2002 at my study site. I used actual humidity data obtained at El Mirage (Western Regional Climatic Center 2010) and assumed that animals started the season with “normal” body water content (70%; Nagy 2004), received no water influx, and continuously exposed all skin (except the venter) to the atmosphere at surface conditions.

Chew and Dammann (1961) provided evaporative water loss rates for *C. s. scutulatus* at two humidities: 0.0 and 3.3 mg/L absolute humidity at 26-27°C. After conversion to relative humidity (RH @ 26.5°C and 1 atm), these two data points were used to produce a linear model of evaporative water loss (EWL) rate per unit of surface area ($g/cm^2/d$):

$$\text{EWL rate} = (-\,0.0479 \cdot \text{RH} + 2.1769)/1000 \qquad \text{[EQ1]}$$

Mautz (1982) provided an equation to calculate skin surface area (SA) of boids and vipers (similar body shapes) in cm^2 from body mass (BM) in grams:

$$\text{SA} = 12.5 \cdot \text{BM}^{0.67} \qquad \text{[EQ2]}$$

Body water content (WC) as mass (WCm) in grams at time *t* (WCm_t) can be calculated as:

$$\text{WCm}_t = \text{WCm}_{t\text{-}1} - ((\text{EWLrate} \cdot \text{SA}_{\text{t-zero}})/1000) \qquad \text{[EQ3]}$$

Note that SA is calculated as $SA_{t\text{-zero}}$ throughout. Even though the animal loses mass as time passes, it does not lose skin as it loses water. As Dmi'el (1985) discovered, cutaneous evaporation per unit of surface area is independent of body mass.

Body mass in grams at time *t* (BM_t) can be calculated as:

$$BM_t = BM_{t-1} - WCm_{t-1} - WCm_t \qquad \text{[EQ4]}$$

Body water content as percent of body mass at time *t* ($WC\%_t$) can be calculated as:

$$WC\%_t = (WCm_t \,/\, BM_t)*100 \qquad \text{[EQ5]}$$

Combining these equations yields:

$$WC\%_t = ((WCm_{t-1} - ((((-\,0.0479 \bullet RH + 2.1769)/1000) \bullet (12.5*BM^{0.67})_{t\text{-zero}})/1000)) \,/\, (BM_{t-1} - (WCm_{t-1} - WCm_t))) \bullet 100 \qquad \text{[EQ6]}$$

SUN AZIMUTHS

The azimuth of the sun (not to be confused with the angle above the horizon) in compass degrees relative to true north was determined for the specific date and time (to the minute) of each observation from the United States Naval Observatory (USNO) website (http://aa.usno.navy.mil/data/docs/AltAz.php; accessed 30 June – 3 July 2012), with Apple Valley, CA, entered for the location. My field estimates of directions were relative to true north (i.e., Central and Johnson Roads); thus, no conversion was necessary for comparisons between my estimates and sun azimuths determined from the USNO website.

SUN AND WIND EXPOSURE

Relative intensity of solar insolation on a landscape scale (i.e., ≥ 10 m resolution) for each daytime observation was calculated from the ground aspect at the location and the sun azimuth for the specific date and time. This value is expressed on a 180^{o} scale, with 0^{o} = maximum intensity and 180^{o} = minimum intensity (Fig. 6). Potential shelter from sun and wind provided by nearby shrubs (microhabitat scale: < 10 m resolution) was calculated from the estimated direction of the snake from the nearest shrub and the sun azimuth or estimated wind direction, computed on the same 180^{o} scale as described above (i.e., 0^{o} = maximum exposure and 180^{o} = maximum shelter).

Using only data from the eleven rattlesnakes recorded in both drought and non-drought at the same wind velocities (rounded to nearest 5 km h^{-1}), mean wind shelter scores (with velocity categories pooled) were first compared using a paired-samples *t*-test. Then the wind shelter scores for drought and non-drought conditions were sorted by animal and then by wind velocity category (5, 10, 15, and 20 km h^{-1}) and mean wind shelter scores within each wind category were compared between drought and non-drought using paired-samples *t*-tests. More informative tests like ANCOVA were not useful because all animals were not represented at the higher wind velocities (due to those events being less frequent), which produced small and asymmetric samples.

I attempted to identify progression of wind shelter-seeking during the drought by dividing the 2002 season temporally into three periods: 1 April–15 June, corresponding to the first third; 16 June–31 August, corresponding to the second third; and 1 September–31 October, corresponding to the last third of the activity season when an

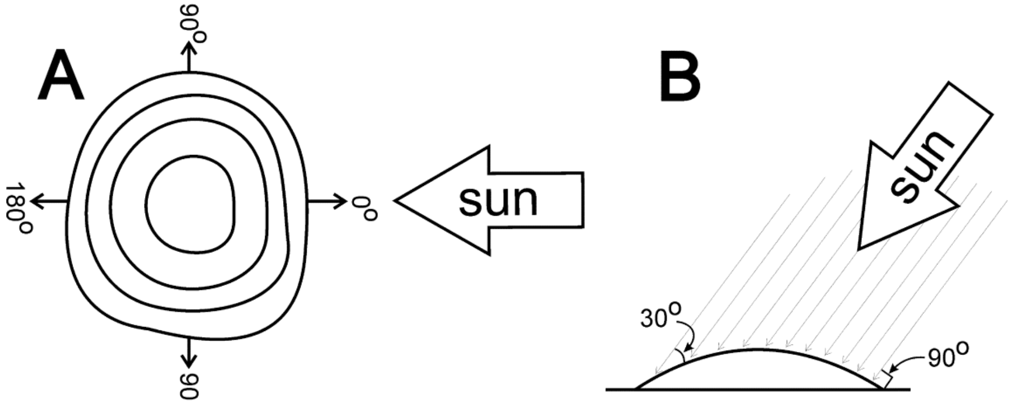

Figure 6. Overhead view (**A**) and lateral view (**B**) of solar energy (insolation) striking a raised topographic feature. I calculated relative insolation from aspect data on a 180° scale (**A**), with 0° = maximum insolation (aspect = sun azimuth) and 180° = minimum insolation (aspect = sun back azimuth). Insolation is most intense when sunlight strikes the surface at 90°, as indicated on the right side of **B**. As the angle of incidence is reduced, insolation is reduced in proportion to the sine of the angle. Thus, the 30° angle indicated on the left in **B** delivers half the energy per unit of surface area as the light striking at 90° on the right.

increase in relative humidity and decrease in air temperature were recorded (Fig. 4). I then used Friedman’s Test (Townend 2002) of multiple related samples to examine mean snake-to-shrub distance and mean *Larrea* association frequency for significant differences in the eleven study animals for which I had data from all three periods.

SELECTION OF AMBUSH POSITIONS

Ambush positions were identified as “pancaked” (a round coil on top of the soil; Fig. 7A), “cratered” (similar to a pancaked coil but partially buried in loose soil, leaving a “crater” upon the snake’s departure; Fig. 7B, C), or “BEAP” (burrow entrance ambush position; Fig. 7D). The mean percentages of observations in each ambush position were calculated for each animal and monthly means were compared between drought and non-drought conditions.

ESTIMATING SKIN AREA COVERED BY COILING AND CRATERING

I could find no previously published estimate of how much exposed skin area is reduced by coiling. After carefully examining my own photos of 71 pancaked *C. s. scutulatus*, it was apparent that a great amount of variation existed in the symmetry and tightness of the coils; thus, the best calculation could only crudely estimate the portion of surface area that was covered by skin-to-skin contact in any given coiled rattlesnake. After measuring scale widths on several live *C. s. scutulatus*, counting scale rows and dorsal blotches in photos, and calculating the likely area of the triangles and ellipses where skin covered skin, I estimated that a coiled rattlesnake reduced its exposed surface area to ca. 50% of the area exposed when it is outstretched. The difference in measured

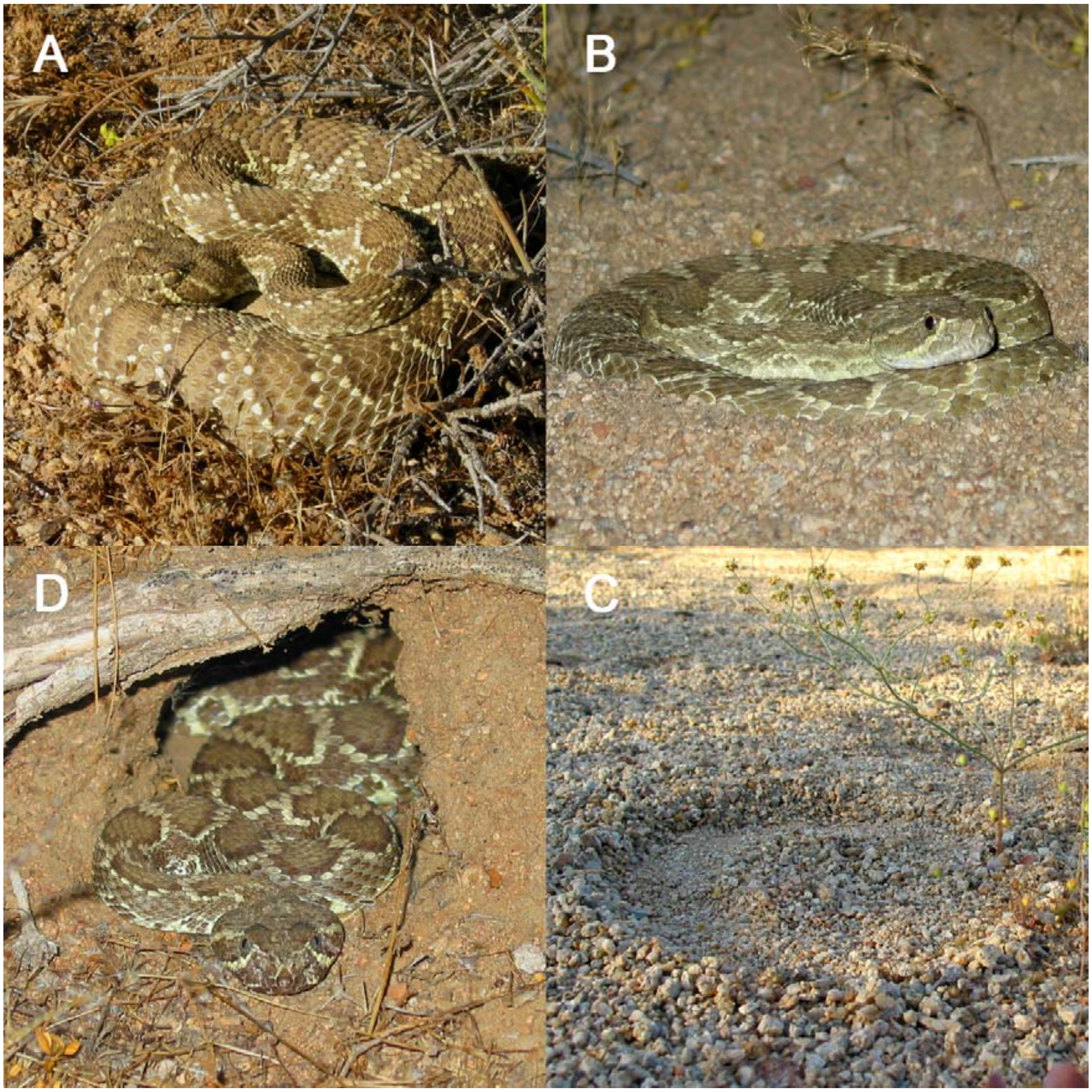

Figure 7. Stereotypical foraging positions: “pancaked” (**A**) on soil surface, “cratered” (**B**) into soil with resulting crater (**C**), and “BEAP” (Burrow Entrance Ambush Position; **D**). See Appendix A.

evaporative water loss between Cohen’s (1975) outstretched and coiled sidewinders suggested a 70% reduction in exposed skin when the snakes were coiled. I have used the median value between my estimate and the value extrapolated from Cohen’s (1975) data: a 60% reduction in exposed skin area produced by pancake-coiling, compared to being outstretched.

Examination of 21 of my photos of cratered rattlesnakes indicates that a great amount of variation also existed in these positions and in the depth to which their flank was covered by soil. It is apparent from the photos and from examining abandoned craters that soil only covered the outside arc of the coil for ca. 35–40% of the snake’s length. The mean number of scale rows (counted laterally across the snakes’ long axis) in my *C. s. scutulatus* sample (*n* = 85) was 26.0 ±0.110SE, range 24–29. Thus, each scale row accounted for ca. 3.8% (1/26th) of the surface area (exclusive of the venter). If cratering covered ca. 37.5% of the snake’s length on one side, each scale row covered by soil reduced exposed surface area by ca. 1.4%.

DATA ANALYSIS

Calculating worst-case dehydration – My evaporative water loss model was intended to estimate a near-worst-case scenario for dehydration of Mohave Rattlesnakes during the summer of 2002 at my study site. Factors taken into consideration included rates of cutaneous and pulmonary evaporation, body mass, skin surface area, body position, air temperature, humidity, air movement, and phylogenetic relationships. While all of these factors could not be incorporated mathematically into the model, they were all addressed in my analyses and discussion.

Refining the data – From the entire data set of 3777 recorded encounters, I culled 1553 observations that were not relevant to these analyses (see Appendix B for details). The remaining data constituted the master data set for these analyses. It described 2224 encounters with 68 male and non-reproductive female *C. s. scutulatus* occurring during the activity seasons (April–October) of 2002, 2003, and 2004 (783, 655, and 786 encounters, respectively). Of these encounters, 2144 were with 20 telemetered animals (mean encounters/snake = 107.8 ±63.84 SD; range 4–201), while the remaining 80 were chance encounters with 48 non-telemetered conspecifics (mean encounters/snake = 1.4 ±0.93 SD; range 1–5). Figure 8 illustrates the relative monitoring periods for the 20 telemetered animals.

Foraging rattlesnakes – From this data set, a subset of foraging rattlesnakes was extracted by choosing only encounters where animals were found in one of the ambush positions (pancaked, cratered, or BEAP).

Using these criteria to identify apparently foraging rattlesnakes is not without controversy, since the pancake coil seems to be the default resting position for these animals. Observations were removed from the foraging data set when snakes were in a pancake coil but clearly involved in some activity besides hunting (e.g., courtship or pre-shed basking). Because snakes have rigid spectacles covering the eyes rather than eyelids, they cannot close their eyes while sleeping. Determination of a motionless snake's level of consciousness is, therefore, a topic of much frustration among herpetologists with little literature on the subject. It is not uncommon to work for a few minutes in close proximity to a coiled rattlesnake, only to elicit a startled response if the

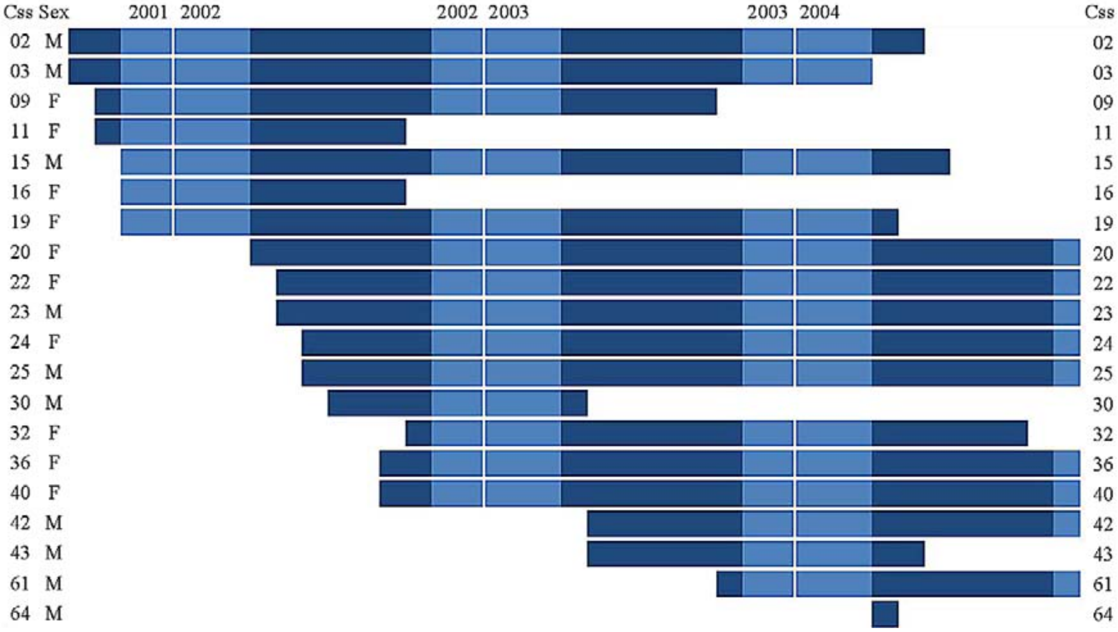

Figure 8. Relative duration of data acquisition for telemetered *C. s. scutulatus* (*n* = 20). Css = animal identifier; light blue = transition and hibernation months (November–March). Telemetry began on 22 August 2001 and ended on 22 November 2004. Drought occurred during 2002, with more normal precipitation returning in 2003 and 2004.

snake is actually touched. As obligatory surface ambushers, it is my hypothesis (although untested herein) that *C. s. scutulatus* typically chooses to rest on the surface in locations and positions that are likely to produce a meal, given tolerable environmental conditions. Even if it sleeps through the passing of an occasional prey animal, it is still more likely to feed successfully than if it retreats into an underground burrow where the chance of foraging success is near zero, although temperature and humidity may be more favorable.

My foraging data set consisted of 1191 encounters (n_{2002} = 470, n_{2003} = 322, and n_{2004} = 399) with 43 *C. s. scutulatus*. Of these encounters, 1161 were with 20 telemetered animals (mean encounters/snake = 58.1 ±36.1 SD; range 3–131), while the remaining 30 were chance encounters with 23 non-telemetered rattlesnakes (mean encounters/snake = 1.3 ±0.85 SD; range 1–4). Where repeated measures tests were used, these data were culled further to observations of only those animals involved in the behavior being assessed during both drought and non-drought periods.

Vegetation survey – I returned to the study site on 28–29 May 2008 to assess several environmental factors, including the density of perennial shrubs. These xeric shrubs are exceptionally slow growing, so the numbers and locations of mature shrubs are not believed to have changed since my field work (Vesek 1980; MacKay 2003). Fifty 10x10 m plots were identified (using random numbers associated with coordinates for their SW corners) within the study area. In the field, each plot was located with the GPS receiver, laid out with compass, measuring cord, and stakes (Fig. 9) and surveyed

Figure 9. Laying out one of 50 sample plots during the May 2008 vegetation survey. Photo by Denise Garland.

for the number, diameter, and taxa of perennial shrubs. The estimated density of each perennial taxon at the study site was extrapolated from these data.

Statistical methods – When comparing drought against non-drought behavior, two-tailed within-subjects *t*-tests were preferred to compare behavioral means produced by animals that had been recorded during both drought and non-drought periods. However, for repeated samples with very small sample sizes or unequal variances, the non-parametric Wilcoxon Signed Ranks test was used. The Friedman’s Test (Townend 2002) of several related samples was used to compare data from the same animals sampled on more than two occasions. Behavioral scores from multiple observations of individual animals were always averaged to eliminate pseudoreplication. A type I error threshold of 0.05 was used to evaluate all statistical results.

I used data from telemetered rattlesnakes exclusively for repeated measures analyses because non-telemetered animals did not produce sufficient numbers of repeated encounters. Where possible, however, data from telemetered and non-telemetered rattlesnakes were pooled because the presence or absence of a transmitter did not produce a significant difference in mean daily growth (ANCOVA, $p = 0.344$; MDC in press), which is presumed to be a good analog for foraging success and, thus, for foraging behavior.

Statistical calculations were carried out with PASW® Statistics GradPack 18 (SPSS Inc., Chicago, Illinois, USA). The Evaporative Water Loss model (Fig. 10) was created in Excel® v. 2002.

RESULTS

MODELING EVAPORATIVE WATER LOSS

Using EQ6 (p. 21) and the humidity data from El Mirage (Western Regional Climatic Center 2010), I modeled the near worst-case scenario for dehydration of three differently-sized rattlesnakes for the period 1 March through 25 September (thus excluding the cloudiness and increased humidity beginning on 26 September). Selected body mass-dependent mathematical functions for evaporative water loss are:

starting body mass 100 g: $y = -0.0005x^2 + 0.0078x + 70$ ($r^2 = 0.999$)

250 g: $y = -0.0003x^2 + 0.0002x + 70$ ($r^2 = 0.998$)

500 g: $y = -0.0002x^2 + 0.002x + 70$ ($r^2 = 0.998$)

where y = percent body water; x = time in days, starting 1 March ($x = 1$)

The model (Fig. 10) shows potential dehydration rates, assuming no water influx during the entire year, starting body water content of 70% (normal = 65–75%; Nagy 2004), and all skin surface (except venter) exposed to surface conditions at all times. Resulting body water content values below Nagy's (2004) normal range (< 65-75%) are presumed to be physiologically stressful. The model suggests that smaller rattlesnakes dehydrate at faster rates than larger ones and, without water influx or some behavioral strategy that reduces evaporative water loss, dangerous levels of dehydration were likely by the end of the summer.

SOLAR SHELTER PROVIDED BY FLORA

In 44 of 194 observations of rattlesnakes when the sun was shining brightly (shadow = sharp; see Appendix A), the direction of the rattlesnake from the shrub was

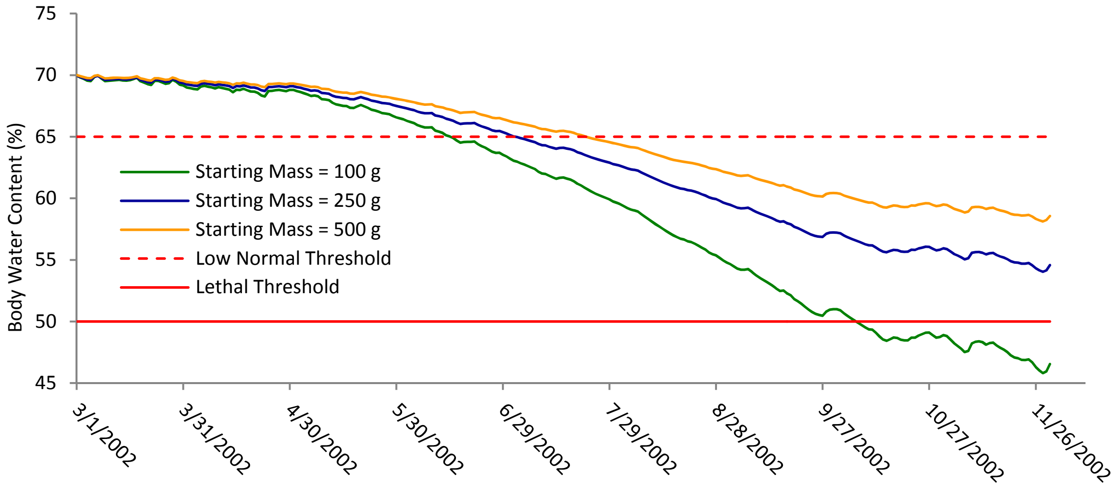

Figure 10. Estimated body water content (%), based on evaporative water loss model and actual humidity data for three hypothetical *Crotalus s. scutulatus* at my study site in 2002. Starting with body masses of 100 g, 250 g, and 500 g, and 70% body water content, these animals drop below the “normal” range (65–75% body water) at 10 June, 29 June, and 17 July, respectively. Death is assured as body water content nears 50% (Nagy 1987).

recorded as "center" (i.e., among the basal stems; see Appendix A), leaving 150 cases with directional data and, thus, numerical solar shelter scores. Nine animals contributed data during drought and non-drought periods, derived from 38 and 50 observations, respectively (mean = 4.9 ±0.84SE, range: 1–12/animal/period). Mean solar shelter scores of 95^{o} ±11.5SE for drought and 81^{o} ±12.5SE for non-drought periods were not significantly different (Wilcoxon Signed Rank Test: Z = -0.533, $n = 9$, $p = 0.594$).

To evaluate the proportion of observations of rattlesnakes in the center of shrubs during bright daylight, I compared the mean proportion of "center" observations for each of the nine rattlesnakes between drought and non-drought periods. A Wilcoxon Signed Rank Test indicated that the difference between drought (0.32 ±0.078SE) and non-drought (0.24 ±0.062SE) proportions was not significant ($Z = -0.474$, $n = 9$, $p = 0.635$).

The correlation between solar shelter scores and distance from the sheltering shrub was not significant during the non-drought period (Pearson's $r = -0.464$, $n = 9$, $p = 0.208$). However, the rattlesnakes tended to locate themselves closer to the shrub canopy (mean 0.1 m, ±0.06SE, range 0.0–0.7, $n = 9$) during the drought when they were on the side of the shrub facing the sun (Pearson's $r = 0.761$, $p = 0.017$; Fig. 11).

SLOPE AND ASPECT

The nine animals observed in bright daylight conditions (shadow = sharp, see Appendix A) during drought and non-drought periods provided data from 54 and 66 observations, respectively (mean 6.6 ±0.98SE, range: 1–14/animal/period). A Wilcoxon Signed Rank Test of the mean aspect-sun shelter scores between drought (114^{o} ±10.6SE)

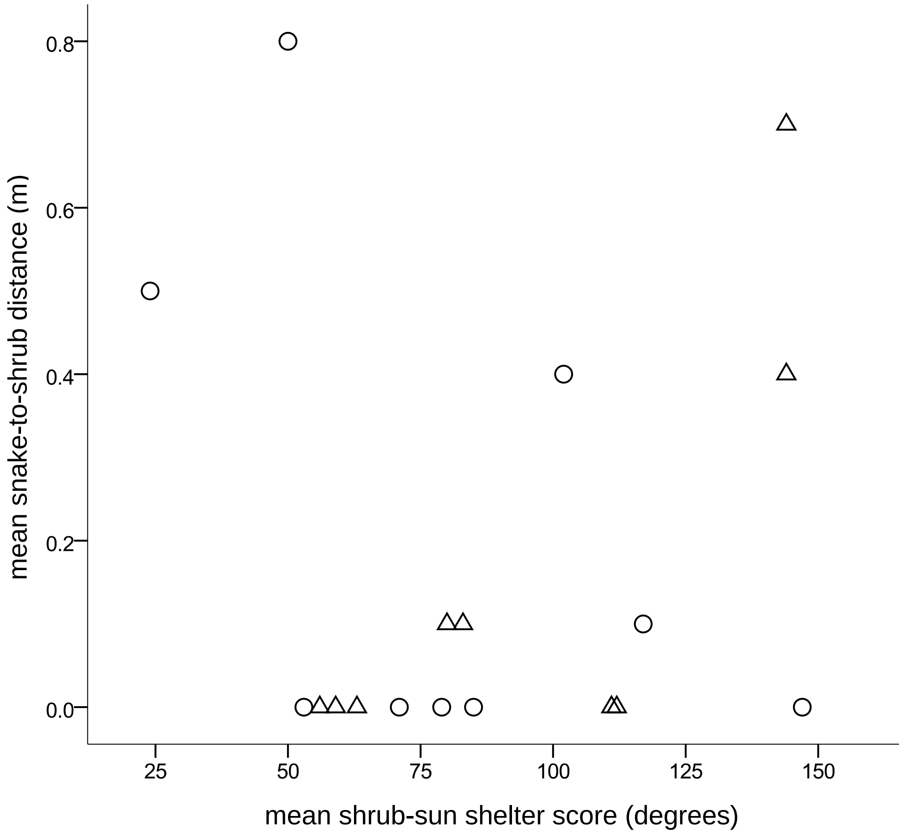

Figure 11. Correlations between means of shrub-sun shelter score (x-axis; 0–180^{o}; see Fig. 6A) and distance from the nearest shrub canopy (y-axis) for repeated measures of nine rattlesnakes. Circles = non-drought period ($p = 0.208$); triangles = drought period ($r = 0.761$; $p = 0.017$).

and non-drought (97^{o} ±11.8SE) observations did not indicate a significant difference (Z = -1.007, n = 9, p = 0.314).

I found no significant difference (Z = -0.474, n = 9, p = 0.635) in mean aspects for foraging rattlesnakes between drought (249^{o} ±9.9SE) and non-drought (251^{o} ±11.4SE) conditions. Similarly, I did not find a significant difference when mean slopes from drought (1.3^{o} ±0.24SE) and non-drought (1.7^{o} ±0.33SE) conditions were compared (Wilcoxon Signed Rank test: Z = -1.342, n = 9, p = 0.180).

A Principal Component Analysis (PCA) was run with slope, aspect, sun air temperature, body temperature, and drought/non-drought as factors. Three principal component (PC) axes were found with Eigenvalues > 1: PC1 = 1.631, explaining 32.6% of variance; PC2 = 1.246, explaining 24.9%; and PC3 = 1.015, explaining 20.3%. A rotated component matrix indicated that sun air temperature and body temperature correlated strongly (0.909 and 0.883, respectively) with PC1, drought/non-drought and aspect correlated (0.775 and 0.557, respectively) with PC2, and slope and aspect correlated (0.710 and 0.708, respectively) with PC3. No additional testable correlations were indicated, and sun air temperature and body temperature are further evaluated below.

DAYTIME AIR AND BODY TEMPERATURES

Mean differences between drought and non-drought data for sun air temperature (26^{o} ±0.74SE and 27^{o} ±1.3SE, respectively) and body temperature (25^{o} ±0.85SE and 26^{o} ±1.2SE, respectively) were not significant (Wilcoxon Signed Ranks tests: Z = -0.776, n = 9, p = 0.438 and Z = -1.380, n = 9, p = 0.168, respectively).

WIND EXPOSURE

The wind shelter data (Table 1) suggest a trend toward seeking more shelter as wind velocity increases, especially during drought (Fig. 12), but the null hypothesis could not be rejected when drought/non-drought scores were compared within wind categories (paired-samples *t*-tests; all $p \geq 0.105$).

However, when wind velocity categories were pooled, mean wind shelter scores for drought conditions were significantly higher than for non-drought conditions (111^o ±5.3SE and 91^o ±4.7SE, respectively; paired-samples *t*-test: $t = -2.600$, df = 10, $p = 0.027$).

<u>Flora associations</u> – Of the 458 rattlesnakes encountered in ambush positions, in both drought and non-drought conditions (pooled), when wind velocity was ≥ 5 km h^{-1}, 72.7% were closest to *Larrea tridentata*, followed in rank order by *Ephedra* ssp. (9.2%), and unidentifiable desiccated shrubs (8.3%); associations with all other perennial taxa were < 2% each. Based on the May 2008 vegetation survey, estimated abundance of these shrubs in the study area was 52.8% *Larrea tridentata* (most abundant), 14.7% *Ephedra* spp. (2nd in abundance), and 6.2% desiccated and unidentifiable (4th in abundance). A goodness of fit test indicated significant differences in shrub associations ($\chi^2 = 145.1$, df = 2, $p < 0.001$).

Differences in mean wind velocity associated with *Larrea*, *Ephedra*, and unidentifiable desiccated shrubs between drought and non-drought conditions were not statistically significant (all $p > 0.062$). Mean distances of foraging rattlesnakes from the

Table 1. Mean wind shelter data (difference between wind and shrub-to-snake directions) for drought and non-drought observations.

	wind velocity (km h^{-1})	*n*	mean wind shelter (^{o})	±SE
Drought	5	11	105.6	8.43
	10	10	104.4	7.85
	15	6	120.0	18.23
	20	2	135.0	0.00
Non-drought	5	11	92.0	4.13
	10	10	86.1	7.05
	15	6	99.4	22.38
	20	2	101.2	78.85

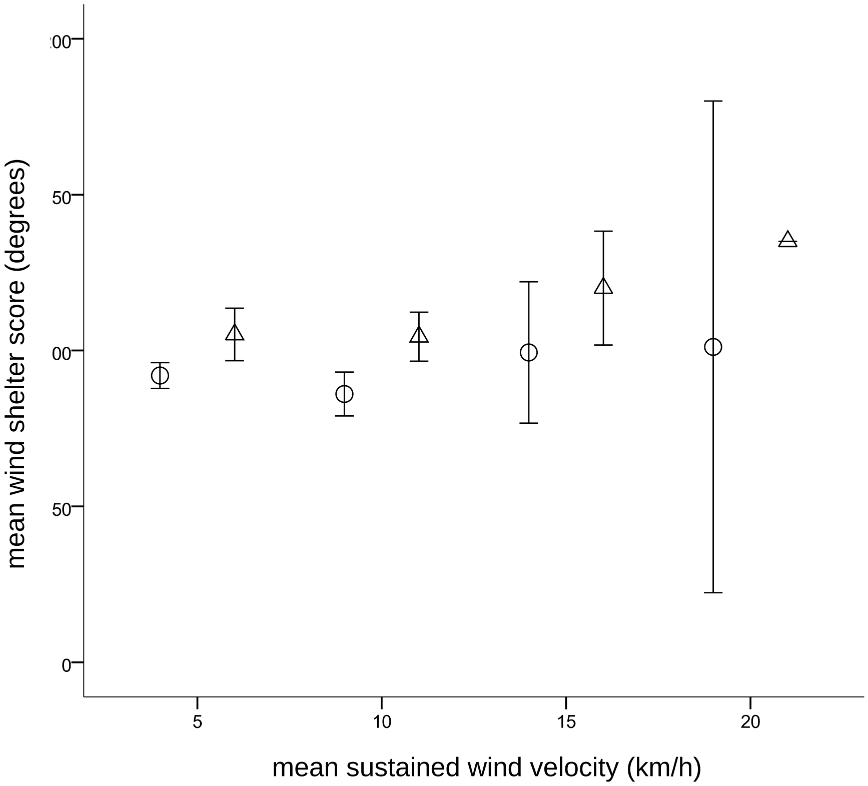

Figure 12. Mean wind shelter provided by closest shrub for paired samples (Table 1) during drought (triangles) and non-drought (circles). Error bars = 1 SE. Wind shelter: 0^o = no shelter; 180^o = maximum shelter.

nearest shrub also were not significantly different among drought and non-drought conditions (all $p > 0.139$).

When drought and non-drought data were pooled and examined between wind categories, correlations were apparent between wind velocity and both snake-to-shrub distance (Fig. 13A) and in the frequency with which the snakes were associated with *Larrea* (Fig. 13B). The differences between wind categories in both snake-to-shrub distance and *Larrea* association frequency were significant (Friedman's Tests; $\chi^2 = 11.060$, df = 3, $p = 0.011$ and $\chi^2 = 7.974$, df = 3, $p = 0.047$, respectively).

The attempt to detect progression of wind sheltering during the summer of 2002 indicated that there were no significant temporal differences in either snake-to-shrub distance or *Larrea* association frequency (Friedman's Tests; both results were identical: $\chi^2 = 0.500$, df = 2, $p = 0.779$).

SELECTION OF AMBUSH POSITIONS

Mean annual percentages of observations of foraging rattlesnakes in pancaked, cratered, and BEAP ambush positions are listed in Table 2. When non-drought years are pooled and compared to the drought data, it is clear that cratering replaced pancake-coiling during the drought, when compared to non-drought conditions (Fig. 14).

The means for repeated measures between the drought and non-drought periods for rattlesnakes in each foraging position are contained in Table 3. When these data were compared, the differences between drought and non-drought in the use of pancaked and cratered positions were significant (paired samples *t*-tests; pancaked: $t = -9.435$, df = 9, $p < 0.001$; cratered: $t = 12.847$, df = 9, $p < 0.001$; BEAP: $t = -1.262$, df = 9, $p = 0.239$).

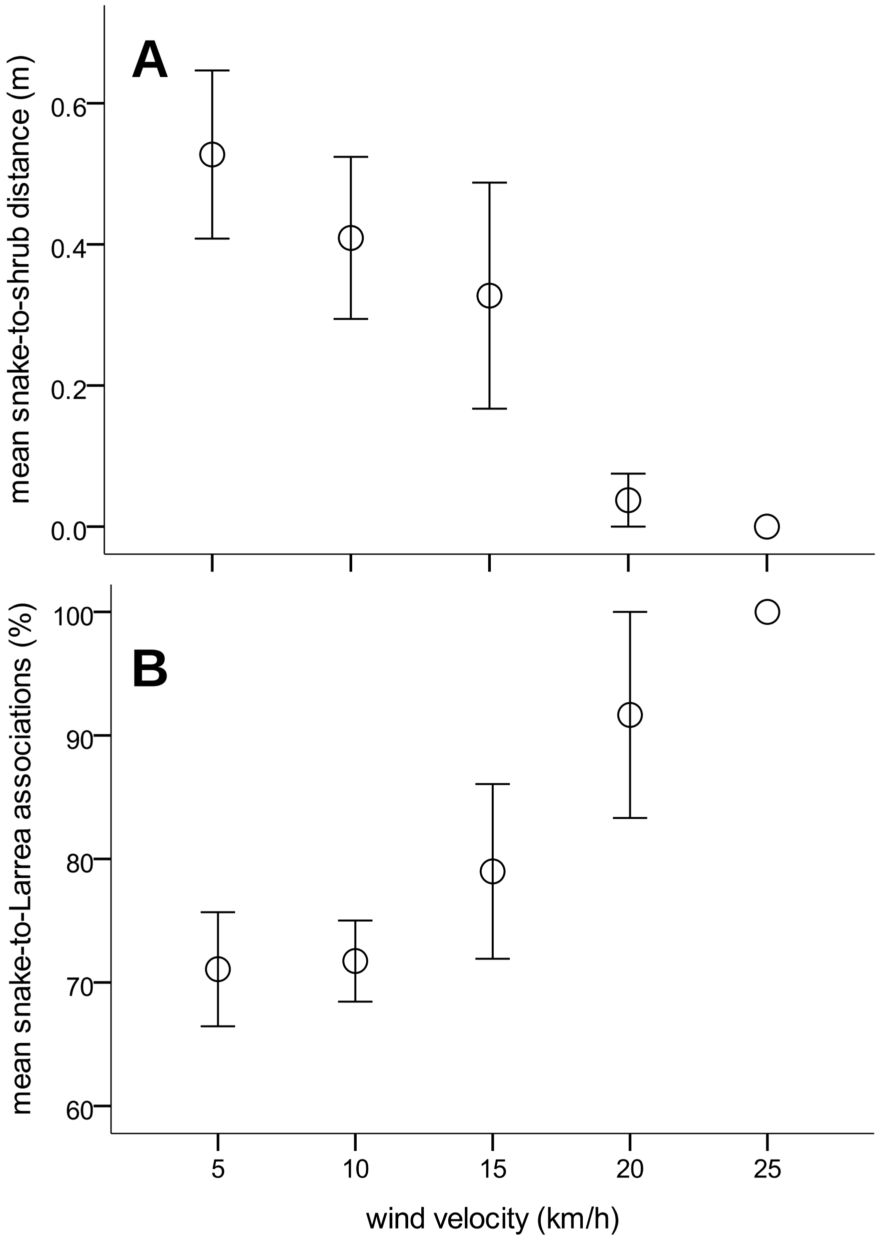

Figure 13. Correlations of wind velocity with mean snake-to-shrub distance (**A**) and with mean percentage of observations where foraging rattlesnakes were nearest to *Larrea tridentata* (**B**) with drought and non-drought data pooled. Error bars = 1 SE.

Table 2. Comparison between years of mean percentage of foraging time spent in each ambush position. BEAP = burrow entrance ambush position.

	2002			2003			2004		
	%	±SE	*n*	%	±SE	*n*	%	±SE	*n*
Pancaked	44.3	6.45	13	86.1	3.56	11	77.3	4.14	8
Cratered	44.5	4.76	13	9.0	3.23	11	3.9	1.13	8
BEAP	11.1	2.61	13	5.0	1.96	11	18.5	3.66	8

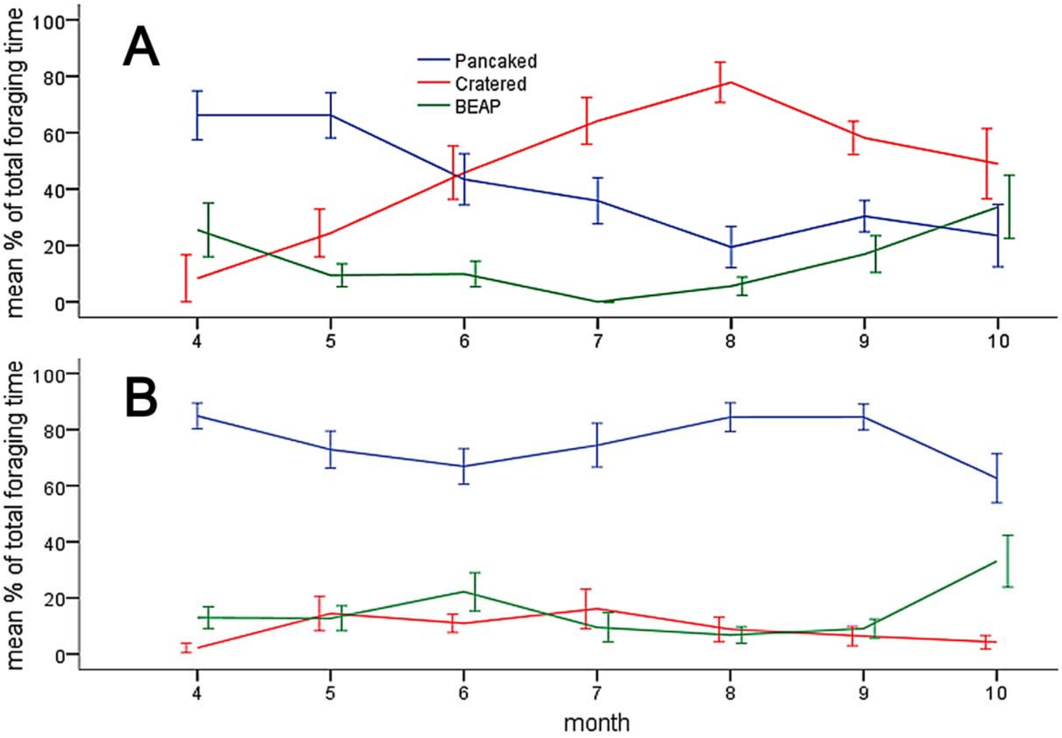

Figure 14. Mean percentages of foraging time from repeated measures data for pancaked, cratered, and BEAP (Burrow Entrance Ambush Position) ambush positions during drought (**A**) and non-drought (**B**) periods. Error bars = 1 SE. The differences between pooled drought and non-drought percentages of pancaked and cratered rattlesnakes were significant (within-subjects *t*-tests, $t = -9.435$, df = 9, $p < 0.001$ and $t = 12.847$, $n = 9$, $p < 0.001$, respectively). The difference between pooled BEAP means was not significant ($t = -1.262$, $n = 9$, $p = 0.239$). See Tables 2 and 3.

Table 3. Comparison of repeated measures between drought and non-drought (2003 and 2004 pooled) of mean percentages of foraging time spent in each foraging position. BEAP = burrow entrance ambush position. Significance values were derived from paired samples *t*-tests.

	drought			non-drought			
	%	±SE	*n*	%	±SE	*n*	*p*
Pancaked	37.4	4.51	10	76.9	1.95	10	< 0.001
Cratered	51.6	3.44	10	8.5	2.79	10	< 0.001
BEAP	11.0	2.16	10	14.7	2.46	10	0.239

DISCUSSION

My analyses suggest that even such a large and robust rattlesnake as *C. s. scutulatus* can become dehydrated in as little as four months in the climatic conditions that existed at my study site in the spring and summer of 2002. Dehydration is greatly accelerated in small rattlesnakes and those starting the season at less than normal body water content.

Although I documented unique rain-harvesting behavior during unpredictable summer thunderstorms (Cardwell 2006), I found no evidence that the animals in this study emerged during the winter to drink (cf. Repp and Schuett 2008). Thus, it is clear that the animals in my study must rely on water that is preformed in their prey and water produced as a byproduct of oxidative metabolism as their only sources of water during an essentially rainless summer.

If, indeed, these animals are obligatory surface ambushers, then it follows that the proximate cause of the behavior I recorded in 2002 was minimization of evaporative water loss while they remained on the surface to hunt, rather than retreating underground where evaporative water loss would have been reduced. In other words, the benefit of water gained by feeding outweighed the cost of water lost by remaining in harsh surface conditions.

My observations are consistent with Cohen's (1975) suggestion that any behavioral modification that would increase (or preserve) the boundary air layer or decrease the amount of exposed cutaneous surface area would enhance water conservation. My data suggest that this population of *C. s. scutulatus* routinely reduces the skin area exposed to dry fluid air by pancake coiling and minimizes the disruption to their boundary air layer by taking refuge from wind behind raised mounds of earth surrounding *Larrea tridentata*, and may do so more frequently and/or consistently during times of water stress. The most profound behavioral change during the drought was the greatly increased use of cratering to protect additional skin from direct exposure to the air as the drought wore on.

EVAPORATIVE WATER LOSS MODEL

My model suggests that small rattlesnakes dehydrate at substantially faster rates than larger ones, an expected function of the ratio of surface area-to-body mass. My model assumes that the animals emerge from hibernation with body water content of 70% and that all skin except their ventral surface is continuously exposed to atmospheric air. It considers cutaneous and pulmonary evaporation (which are continuous obligatory processes) but does not include relatively large occasional water losses due to defecation and ecdysis.

According to Nagy (2004), desert reptiles do not have field metabolic rates (energy expended/day/g) that are substantially lower than similar non-desert reptiles. However, their water flux rates (rate of water in/out) are as much as 50% lower than similar non-desert reptiles (Nagy and Peterson 1988). Desert reptiles are able to survive in such dry environments largely by minimizing their water requirements through behavioral adaptations that slow water loss (Nagy 2004).

When estimating cutaneous evaporation, only the skin surface area in direct contact with fluid air is relevant; the ventral surface upon which the body rests is not in direct contact with the atmosphere. In presenting his formula for “mass-area scaling” for boids and vipers, Mautz (1982) does not mention whether or not his formula includes the ventral surface. In an attempt to resolve this question, I crudely calculated the entire surface area of a 50 cm (100 g) hypothetical rattlesnake, using cones to approximate the shape of the snake, yielding an estimated 364 cm^2. The Mautz (1982) formula ($SA = 12.5 \bullet BM^{0.67}$) yields a surface area of 273 cm^2 for a 100 g snake, or 75% of my estimate. My mid-body measurements of a typical live adult *C. s. scutulatus* yielded a girth of 10.1 cm and a venter width of 3.2 cm, indicating that the non-ventral portion of the girth was 68% of the total. Based on these rough data, I believe that the Mautz (1982) formula, and therefore my dehydration model (Fig. 10), most closely approximates surface area exclusive of the venter.

SHRUBS AS SHELTER FROM INSOLATION

My data failed to detect a significant difference in foraging rattlesnakes’ mean orientation to nearby shrubs in relation to the direction of bright sunlight (solar shelter score; see Fig. 6A) between drought and non-drought periods. Additionally, foraging rattlesnakes were not found at the center of a shrub differently during drought and non-drought conditions.

While no correlation was found between the mean insolation shelter scores and mean rattlesnake-to-shrub distances during the non-drought period, the correlation was significant during the drought year. The mean shrub-to-rattlesnake distance during the drought was 0.1 m (±0.06SE, range 0.0–0.7, $n = 9$). Of the nine rattlesnakes included in these calculations, the mean shrub-to-rattlesnake distance for five of them was 0.0 m, which indicates that they were under the shrub's canopy but not among the basal stems. The significant correlation was positive between solar shelter score and distance from the shrub, meaning that they tended to be farther away from the center of the shrub when on the side away from the sun and they were under the canopy more frequently when on the sunny side of the shrub. This finding suggests that the rattlesnakes were less tolerant of insolation during the drought than during the non-drought period. Since sun air temperature values were not significantly different between drought and non-drought, this finding may suggest an effort to avoid increased cutaneous evaporation due to vasodilation in the skin caused by increased skin temperature (Cohen 1975).

SLOPE AND ASPECT

Bennie et al. (2008) demonstrated experimentally, corroborated with observational data, that slope and aspect of the ground alter the effect of insolation on soil temperature and moisture and, therefore, on microclimate at the soil surface. However, my data fail to demonstrate a difference between drought and non-drought behavior when evaluating slope and aspect on a landscape scale. Mean relative insolation based on aspect choice (i.e., the difference between sun azimuth and aspect angle) was not different between drought and non-drought years.

The rattlesnakes usually occupied landscape-scale locations with aspects close to WSW (247.5^o) during both drought and non-drought, which produces near maximum insolation during the afternoon on sunny days. Sun azimuths rotated across the southern sky, between extremes of 68^o at dawn and 297^o at sunset (ENE–WNW). Substantial areas of the study site face between NW–N–NE, especially on the south side of the major ephemeral washes (see Fig. 3), yet there is no indication that the snakes reduced their potential insolation exposure by seeking out these areas during either drought or non-drought conditions, suggesting that either the difference in insolation was trivial or some other factor produced a cost-benefit choice that rendered remaining in a relatively high insolation area preferable.

DAYTIME TEMPERATURE COMPARISONS

Previous work has shown that cutaneous evaporation increases with air temperature in squamate reptiles, likely due to vasodilation in the skin. Dmi’el (1985) showed that a 10°C increase in air temperature produced a 35% decrease in water vapor density, which increased the evaporative water loss rate. Cohen (1975) showed experimentally that evaporative water loss rates in desert rattlesnakes were increased when air temperature was increased and, separately, that drug-induced cutaneous vasodilation increased evaporative water loss.

However, comparisons of sun air temperatures and of core body temperatures measured at daytime encounters with rattlesnakes in this study did not indicate significant differences between drought and non-drought conditions. It is worth noting that monthly mean temperatures during drought and non-drought periods recorded near my study site were similar (Fig. 4A).

In future efforts, it would be useful to control analyses of solar shelter (by flora, aspect, and slope) for body temperature. There was no significant correlation in these data between solar shelter and sun air temperature but my analysis did not account for cool snakes that might have recently emerged from a burrow. Nonetheless, small sample sizes prohibited dissecting these data further.

SHRUBS AS SHELTER FROM WIND

My analyses indicate positive correlations between increasing wind velocity and two behaviors: the frequency with which *C. s. scutulatus* associated with *Larrea tridentata* and the degree to which the snakes put the shrub between themselves and the wind (Fig. 13). Both of these behaviors occurred during the non-drought period but were exaggerated during the drought.

The study animals were associated with *Larrea tridentata* significantly more frequently (72.7%) than expected (with drought and non-drought data pooled), based on my estimate of abundance (52.8%) at the study site. When wind velocities were pooled, wind shelter scores (0^{o}–180^{o}) were significantly greater during the drought than non-drought (110.0^{o} ±5.63SE and 92.1^{o} ±6.57SE, respectively). When means of drought and non-drought observations within each wind category (Table 1) were compared, my data suggested that the snakes sheltered farther behind the shrubs as wind velocity increased ≥ 10 km h^{-1} (Fig. 12) but the data did not support rejection of the null hypothesis.

When the drought data were divided into temporal thirds, differences between these periods in mean snake-to-shrub distances and mean *Larrea* association percentages of eleven study animals were not significant. Nonetheless, when drought and non-drought data were pooled, the rattlesnakes were found to have associated with *Larrea* more frequently and moved closer to them as wind velocity increased (Fig. 13). While the differences in wind shelter scores between drought (106^{o} at 5 km h^{-1}–135^{o} at 20 km

h^{-1}) and non-drought (92^{o} at 5 km h^{-1}–101^{o} at 20 km h^{-1}) may not appear to have practical value (i.e., what is the value of being beside the shrub relative to wind direction?), the unique life history and morphology of *Larrea tridentata* may explain these findings.

Larrea tridentata is one of the longest-lived extant organisms on the planet, with some living individuals believed to be > 10,000 years old (Vasek 1980). Over time, they accumulate detritus and wind-blown soil beneath their foliage, creating raised mounds of soil ("coppice dunes" per McAuliffe et al. 2007) from which their trunks protrude (Fig. 15). Thus, while being near but next to most shrubs growing on flat ground would produce little shelter from wind coming at < 180^{o} relative to the shrub, angles > 90^{o} to mature *Larrea tridentata* relative to wind direction often puts the rattlesnake on the backside of an earthen mound relative to the wind, although the shrub itself may contribute little to wind shelter.

These data suggest that *C. s. scutulatus* routinely shelters from wind behind the coppice dunes surrounding *Larrea tridentata* but the behavior is more pronounced in times of water stress.

Shelter from wind helps to preserve a boundary layer of stagnant moist air next to the skin. Such a layer next to the skin of squamate reptiles has been shown to slow cutaneous evaporation in xeric environments by providing a buffer in the gradient between the relatively moist epidermal tissue and the drier air. At the air-skin interface, water molecules change phase from liquid to vapor continuously, unaffected by the moisture gradient. However, the rate of simultaneous condensation from vapor to liquid

Figure 15. A large *Larrea tridentata* (creosote bush) with typical large earthen mound (“coppice dune” per McAuliffe et al. 2007) rising beneath the canopy of the shrub from the surrounding terrain.

is directly related to the temperature and water vapor pressure of the air next to the skin. Wind disturbs or removes this boundary layer and increases the moisture gradient between skin and air, thus decreasing the condensation rate of atmospheric water into the skin. Wind, therefore, increases cutaneous evaporation, and the effect is intensified with increasing velocity (Cohen 1975; Dmi'el 1985; Lillywhite and Sanmartino 1993).

SELECTION OF AMBUSH POSITIONS

My analyses indicate a steady increase in the mean monthly use of the cratered ambush position between April and August 2002, eventually rising to 77.8% of observations in August, compared to 8.8% in August during pooled non-drought conditions (Fig. 14), with the cratered position essentially replacing the pancaked position during the drought.

The progressive increase in cratering between April and September, 2002, demonstrates a robust inverse relationship with the progressive dehydration of the study animals predicted by my evaporative water loss model (Fig. 10), including a corresponding correction in late September, when increased humidity likely moderated the rate of evaporative water loss. These results demonstrate perhaps the most profound difference between drought and non-drought behavior and the closest correlation between the predicted dehydration of the animals and month-to-month behavioral change.

The significance of the amount of exposed skin to the rate of evaporative water loss in squamate reptiles has been well established (e.g., Cohen 1975; Mautz 1982; Dmi'el 1985; Nagy 2004). In particular, Cohen (1975) showed by carefully controlled and replicated laboratory experiments that the mean evaporative water loss rate of outstretched sidewinders (*Crotalus cerastes*; a desert rattlesnake sympatric with *C. s. scutulatus*) was significantly greater than when the same snakes were allowed to coil (3.262 and 0.994 mg g^{-1} hr^{-1}, respectively; $p < 0.05$).

The rattlesnakes cratered deepest in my observations, such as the animal in Figure 7B, had ca. 6 scale rows showing above the sand (counting from the dorsal midline), leaving ca. 7 buried (26/2 rows per side). Thus, using my estimate of each buried scale row reducing exposed skin area by ca. 1.4%, I estimate that the rattlesnake in Figure 7B reduced its exposed surface area ca. 10%, in addition to the ca. 60% (the median between my calculations and Cohen's 1975 data) reduction achieved by pancake coiling alone. It is also worth noting that although soil does not cover the interior surfaces of the coils when a snake is cratered, air flow is certainly more restricted than on the outer surfaces that are directly exposed to environmental air movement.

KANGAROO RATS AND WATER

Dipodomys spp. (Heteromyidae), primarily *D. merriami* (Merriam's kangaroo rat), made up ca. 64% (by mass, based on fecal analysis) of the study animals' diet (MDC unpublished data). These ubiquitous desert granivores gather seeds dropped by various plants (primarily *Larrea tridentata*) and cache them for use during times of low production (Nagy and Gruchacz 1994; Price et al. 2000). They remain active, mostly underground, year-around, including during freezing winters and summer droughts. The environment inside *Dipodomys* burrows during hot weather is uniformly cooler and more humid, especially in the daytime, than surface conditions (Kay and Whitford 1978;

Nagy and Gruchacz 1994; Hawkins 1996). *Dipodomys merriami*, in particular, scatter-caches its seeds outside its burrow and thus must occasionally subject itself to harsh environmental conditions (and rattlesnake predation) to retrieve them (Randall 1993; Nagy and Gruchacz 1994; Leaver 2004). Previous studies have shown that adult kangaroo rats suffer little mortality during droughts, although reproduction is severely curtailed (Nagy and Gruchacz 1994). Kangaroo rats therefore provide a reliable source of energy and water during drought for predators like *C. s. scutulatus* and *Dipodomys* burrows offer relatively cool moist refugia when above-ground conditions are hot and dry.

STUDY LIMITATIONS

My study is limited by small sample sizes in two ways. First, despite a robust number of documented encounters with *C. s. scutulatus* (*n* = 3777 over 40 months), the realized *n* was often quite small after eliminating irrelevant encounters and especially when selecting specific behaviors recorded during specific weather conditions, in addition to usually being limited to only those animals observed in both drought and non-drought conditions. The result was the frequent use of less powerful non-parametric statistical methods and increased opportunity for type II error.

Secondly, only one drought season is represented in these data. The correlation between the behavior recorded during 2002 and lack of precipitation would be more convincing if there were multiple drought years available to be averaged and compared to pooled non-drought years.

Additionally, such a study would benefit greatly from a recording weather station located within the study area. In particular, measurement of rainfall at the study site would remove much of the uncertainty about how much precipitation falls and when it occurs.

Finally, my evaporative water loss model (Fig. 10) is based on only two data points derived from Chew and Dammann (1961). Although these data are apparently the product of a carefully controlled experiment that used *C. s. scutulatus* as the model animal, they produce only a linear function. Clearly, the model would benefit from a more robust experimental data set.

Nonetheless, my data and analyses suggest likely ways that these rattlesnakes coped with the desiccating effects of the drought and they provide a valuable basis for future observational studies, as well as manipulative experiments to establish cause-and-effect related to some of the documented behaviors.

CONCLUSIONS

According to Ken Nagy (1988):

> "It is possible, even likely, that a given species does things differently from year to year, in response to the highly variable climates that are characteristic of many deserts."

<u>Regarding Hypothesis 1</u> – The study animals select ambush locations with slope and aspect that minimizes exposure to solar heat in proportion to their degree of water stress:

My data do not support this hypothesis on a landscape scale. However, my analyses suggest that the rattlesnakes moderate exposure to insolation on a microhabitat scale by associating with *Larrea tridentata* more frequently than expected, locating themselves on the earthen mounds surrounding *Larrea* and moving under the shrubs' canopies more consistently when on the sunny side of the shrub during times of water stress.

Regarding Hypothesis 2 – The study animals reduce their wind exposure in proportion to their degree of water stress:

My data support this hypothesis, suggesting that these rattlesnakes use the earthen mounds surrounding *Larrea tridentata* as shelter from wind during both drought and non-drought periods, moving farther behind and closer to the shrubs as wind velocity increases. This behavior appears to be more pronounced when the rattlesnakes are water stressed.

Regarding Hypothesis 3 – The study animals use "cratering" (partially burying their coiled body in loose soil) to reduce skin area exposed to dry fluid air in proportion to their degree of water stress:

My data support this hypothesis, with indications that the rattlesnakes reduce cutaneous evaporation by up to ca. 10% by cratering into the soil while they sit and wait to ambush prey on the surface, which is their only source of water during drought. The frequency of cratering corresponds to the theoretical dehydration of the rattlesnakes as the waterless summer progresses.

APPENDIX A

SERIAL DATA DEFINED

Serial data fields, with menus and definitions, are listed below. This is a truncated list containing only those fields applicable to this thesis. At the beginning of the field work (August 2001), 46 observations were being recorded at each encounter. By the final field season, five additional data fields had been added, so that standardized data were being recorded for fifty-one fields at each encounter in 2004. With 3777 encounters (with 80 different rattlesnakes) recorded over forty months, the master data set contained 181057 data entries at the end of 2004.

Field	Definition/menu
Css#	Sequentially assigned study animal identification number
Sex	M/F
Transmitter (Tx)	Is the animal telemetered? Y/N
Date	dd.mmm.yy
Time	Pacific Standard Time (GMT -8 h; Daylight Savings Time is ignored)
Observation Category	“Observation” – confirm previously documented animal’s location and collect associated data; "Initial Capture" – first time capture; "Recapture" – removal of a previously documented animal from the field;

	"Release" – return a captured animal to the place of capture;
	"RF Signal Only" – record radio frequency signal without confirming animal’s location;
	"Mortality Event" – death of an animal, including road kills on the study area boundary;
	“UTL” – unable to locate an animal or its RF signal;
	"Other" – a catch-all category for events that do not fit into other categories (see hand-written notes)
Easting	5-digit UTM easting from GPS receiver (using WGS84 datum)
Northing	5-digit UTM northing from GPS receiver (using WGS84 datum)
GPS Error	Estimated GPS error taken from GPS receiver after “averaging”
Distance Moved	since last observation (calculated and entered later).
1st Tx Interval	Transmitter pulse interval, in ms, established by timing eleven beeps (ten intervals) with a stopwatch and multiplying by 100.
2nd Tx Interval	Repeat
3rd Tx Interval	Repeat
Tx Mean	The arithmetic mean of the three Transmitter Intervals (automatically calculated by the handheld software)
Calculated T_b	Body temperature calculated from mathematical “best fit”

	model derived from manufacturer's calibration data and corrected, if necessary, based on my water bath test(s)
T_{sh}	Air temperature (^{o}C) in full shade at 1 cm above the ground
T_{su}	Air temperature (^{o}C) in full sun at 1 cm above the ground
Overcast	Estimated percent of sky obscured by clouds in 10% increments
Shadow	This was an unsophisticated effort to record radiant solar energy. I held an arm out with my hand two meters above the ground and spread my fingers, then entered one of the following: "None" – no shadow is visible (Moon shadows don't count); "Sharp" – shadow of individual fingers is visible (except "variable" below); "Diffuse" – shadow of the arm is visible but the fingers are not (except "variable" below); "Variable" – clouds are causing shadow conditions to fluctuate
Wind velocity	Rounded to nearest 5 km h^{-1}, measured with Kestrel 1000® hand-held anemometer set to measure average wind speed (measure for $\geq$15 seconds)
Wind direction	Estimated 16-point compass direction from which the wind is coming

Lighting	Enter “Day”, “Night”, or “Twilight” (i.e., nautical twilight) as determined for each date from the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php)
Moon %	The percentage of full moon illumination, given the date and geographic coordinates, as determined by the shareware program “Moonrise” by Dr. Bruce Seidell (no longer available)
Moon visible	Y/N, depending on whether it is actually above the horizon, obscured by clouds, etc.
Activity	This is a crude blend of observed physical activity and perceived stimulus; most observations will fall into “Other” because it is not clear why the animal is in a particular position. Enter one of the following: "Moving" - crawling from one place to another but does not fit another category; "Predation" –animal is obviously engaged in acquiring prey (striking, scent-trailing, swallowing; not just in ambush position); "Courting" –courtship and/or copulation (either active or passive involvement); "Thermoregulation" – usually basking, when the motive seems obvious (e.g., mid-winter);

	"Ecdysis" – shedding, including pre-shed inactivity (usually identified afterward); "Hydrating" – drinking; "Defense" – defensive behavior due to natural stimuli (not in response to me); "Parturition" – birth, including pre/post-parturition activities; "Winter dormancy" – animal is inactive for prolonged periods during the winter; "Other" –animal is visible but the nature of (motive for) the activity is unclear; "Out of Sight" – animal is not in sight and activity cannot be inferred by other circumstances (e.g., ecdysis or winter dormancy)
Body Position	Enter one of the following: "Outstretched" – as in rectilinear locomotion; nearly straight "Pancaked" – flat round resting coil on top of the substrate, leaving no mark “Cratered” – similar to a pancake but the margins of the coil have been worked into the substrate, leaving a characteristic crater after the animal departs; also includes utilization of a pre-existing depression "Serpentine" –consecutive sigmoidal curves

	"BEAP" – Burrow Entrance Ambush Position; head and neck protruding from a rodent burrow with majority of the body inside the burrow "Periscope" – an alert position with the animal's head held aloft by several centimeters of straight neck protruding nearly vertically from a burrow "Other" – animal is visible but in some other position (e.g., during copulation) "Unknown" – animal is out of sight
Animal Facing	16-point direction the animal's face is pointing if not moving; the direction the snake is traveling if moving; or "Unknown" if the snake (or its head) is out of sight
Sun Exposure	Enter one of the following: "Full Sun" – full sun "Shade" – full shade (in otherwise sunny environment) "Dappled Sun" – filtered sun (e.g., through foliage) without large areas of direct sun "Sun/Dappled" – part dappled sun and part full sun "Sun/Shade" – part full sun and part full shade "Dappled/Shade" – part dappled shade and part full shade "None" if it is night or the animal is out of sight underground

Overhead Environment	"Foliage" – vegetation overhead (at any height) including anywhere within the overhang radius of a shrub, whether or not a branch is directly overhead "Clear" – clear sky directly overhead "In Burrow" – underground in a burrow (whether visible or not) “Debris” – under a manmade object like lumber or trash "Other Soil" – under an escarpment or other overhanging soil (besides in a burrow) "Other Stone" when the animal is under a stone (not in a burrow)
Nearest Flora	Pick the shrub, cactus, or tree yucca (annuals excluded) nearest the rattlesnake from the drop-down menu: *Yucca schidigera* (Liliaceae: Mojave yucca) *Yucca brevifolia* (Liliaceae; Joshua tree) *Larrea tridentata* (Zygophyllaceae; creosote bush) *Ephedra viridis* (Ephedraceae; Mormon tea) *Thamnosma montana* (Rutaceae; turpentine broom) *Lycium cooperi* (Solanaceae; desert thorn) *Salazaria mexicana* (Lamiaceae; bladder sage) *Atriplex canescens* (Chenopodiaceae; four-wing salt bush) *Ambrosia dumosa* (Asteraceae; burrow-weed)

	Coleogyne ramosissima (Rosaceae; blackbush) *Grayia spinosa* (Chenopodiaceae; hop-sage) *Eriogonum fasciculatum* (Polygonaceae; desert buckwheat) *Hymenoclea salsola* (Asteraceae; cheesebush) *Krascheninnikovia lanata* (Chenopodiaceae; winter fat) *Cylindropuntia echinocarpa* (Cactaceae; silver cholla) *Cylindropuntia ramosissima* (Cactaceae; pencil cholla) *Opuntia basilaris* (Cactaceae; beavertail cactus) *Echinocereus* ssp. (Cactaceae; hedgehog cactus) *Ferrocactus* sp. (Cactaceae; barrel cactus) “unid-desiccated” – desiccated shrubs not readily identified “unid-living” – identifiable living shrubs not on the menu (ID or describe in written field notes)
Distance from Nearest Flora	Estimated distance to nearest 0.1 m between the shrub’s overhang to the snake; if snake is under overhang, enter “0”
Direction from nearest Flora	Estimated 16-point direction <u>from</u> the center of the shrub <u>to</u> the rattlesnake; “Center” if the snake is among basal stems; or "Unknown" if the snake is out of sight
Height of Nearest Flora	Estimated height to nearest 0.1 m
Nearest Burrow Taxon	Select one of the following from the drop-down menu: “*Dipodomys*” – for burrows that appear to be *Dipodomys* /

	Ammospermophilus (ca. 30–50 mm diameter) “*Vulpes*” – for burrows that appear to be (or have been) kit fox burrows “*Spermophilus*” – for California ground squirrel burrows “Other” – for any other burrow (explain in narrative field notes)
Additional Narrative	“Y” if data is supplemented by additional hand-written notes; otherwise “N”

APPENDIX B

OBSERVATIONAL DATA REMOVED FROM THESE ANALYSES

From the entire data set of 3777 observations, I removed the following data from consideration in these analyses:

All winter observations: These December–February observations consisted of infrequent visits to record body temperatures of hibernating rattlesnakes, computed from their radio pulse intervals, and associated above-ground conditions.

All November and March encounters: November and March proved to be transition months between the active season and hibernation, during which actual ingress and egress dates varied greatly between individuals and were often characterized by “false starts” when animals would appear to have entered or emerged from their hibernacula, only to re-emerge or become inactive again for a short time.

All “unnatural” behavioral encounters: these included releases after processing, mortality events (although natural events, they contributed nothing to behavioral observations), and encounters where either snakes could not be located or their radio signal was recorded without visiting their location.

Reproductive females: three telemetered females (Css20, 22, 42) produced offspring in 2003 and pregnant female rattlesnakes are well known to fast while thermoregulating most of the year before parturition around mid-September and there is some evidence that evaporative water loss rate is significantly lower in pregnant females than conspecifics (MDC unpublished data); non-reproductive females are *a priori* assumed to behave similarly to males regarding foraging for their energy and water requirements.

Debilitated snakes: Some data were removed from behavioral consideration because the animals became severely debilitated; Css09 (female; 03-24 September 2003) suddenly made a long highly uncharacteristic straight-line move out of the study area and disappeared into a roadside rock fill from which her desiccated carcass was excavated several weeks later, cause of death is undetermined due to her condition; Css32 (female; all after 04 March 2004) went underground and immobile most of the summer, failing to emerge to forage or hydrate during summer rain. When finally observed and captured in August, she was severely underweight and dehydrated and had missed a shed, retaining an old exuvium (she was successfully rehabilitated and released but her 2004 behavioral data was discounted); Css43 (male; all of 2004) was found severely underweight, dehydrated, and on the surface in near freezing weather in early February 2004. Despite two recaptures followed by rehabilitation and releases over several months, he failed to thrive and was eventually euthanized.

Miscellaneous: Data for Css40 (female; 16 September 2004 only) was discounted because she remained in a burrow I selected for her when I released her the day before, several dozen meters from her capture site after processing, due to the persistent presence of a kit fox and no immediately available rodent burrows at her capture site. Instead, she was released into a nearby rodent burrow where she was inaccessible to the fox. By the next encounter, she had moved and presumably reestablished herself in her preferred habitat niche and only one day’s data was discounted.

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