A Comparative Study of Hunted vs. Unhunted Populations of the Twin-Spotted Rattlesnake

David B. Prival, Matthew J. Goode, Don E. Swann, Cecil R. Schwalbe, Michael J. Schroff, and Robert J. Steidl

Wildlife and Fisheries Science, School of Renewable Natural Resources,
University of Arizona, Tucson, Arizona 85721

FINAL REPORT

IIPAM I97040

30 September 1999

Heritage Program
Arizona Game and Fish Department
2221 West Greenway Road
Phoenix, Arizona 85023

DISCLAIMER

EXECUTIVE SUMMARY

Twin-spotted rattlesnakes (*Crotalus pricei*) are a small-bodied, montane species with a limited distribution in the U.S. Due to their rarity and a black market demand for rattlesnakes as pets, twin-spotted rattlesnakes are protected by law in Arizona. Nonetheless, they are collected frequently on talus slopes adjacent to Barfoot Park in Arizona's Chiricahua Mountains. We investigated the impact of collecting on the snake population at Barfoot and gathered information about the ecology of this almost unstudied species.

We captured and marked 109 *C. pricei* at Barfoot and three unhunted sites in the Chiricahuas. Barfoot had a higher density of snakes than the other sites, but on average the snakes were 38.1 mm smaller at Barfoot. There are several possible explanations for this difference in snake size, one of which is intense collecting pressure.

Mating and parturition in twin-spotted rattlesnakes occurred in August and early September. Litters are probably from matings that occurred the previous year. Sceloporine lizards are the most common prey item for twin-spotted rattlesnakes, found in 71% of fecal samples collected.

Radiotelemeters were implanted surgically into 16 snakes to determine activity patterns and obtain other behavioral data. Male activity patterns varied greatly over the study, with much greater movement in 1998 than 1997, possibly related to a drier late summer in 1998. Gravid females moved little between mid-July and the time we suspect parturition occurred, in late August and early September. Some winter activity was observed in both twin-spotted rattlesnakes and their primary prey, mountain spiny lizards (*Sceloporus jarrovii*).

Barfoot has been the primary collecting locality for *C. pricei* throughout the 20th century. We estimate that almost 90 people searched for this protected species at this site between July and September during the two years of the study. Evidence of habitat disturbance was found at Barfoot that was absent on other talus slopes. We recommend establishing a long-term monitoring program for snakes at this site, in addition to continued anti-poaching law enforcement operations, to ensure the continued survival of this population.

INTRODUCTION

WILDLIFE TRADE

Arizona's small montane rattlesnakes have been collected illegally for the pet trade since they were first protected over 30 years ago (Martin 1974, Johnson & Mills 1982). However, the effects of these activities on snake populations are unknown. Overexploitation of wildlife is a major threat to vertebrate biodiversity, second only to habitat loss and degradation (Primack 1998). Overexploitation affects 37% of the threatened vertebrate species identified under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and accounts for 23% of past extinctions for which the cause is known (IUCN 1980, Groombridge 1992). Today, overexploitation exists largely as a result of a growing international trade in wildlife and wildlife products.

This trade in wildlife will likely drive many species to extinction within the next few years (e.g., Matthiessen 1987, Thapar 1996). Estimates of the annual value of the international trade in wildlife and wildlife products vary from $8 billion (Geist 1994) to $20 billion (Swanson 1992). There is even less agreement on the annual value of the illegal trade in these commodities, ranging from $3 billion (Bowles 1996) to $20 billion (Scott 1996).

Reptiles constitute one of the largest components of this commercial trade (Brazaitis 1986). In fact, overexploitation has been identified by at least one group as the most serious threat faced by reptiles worldwide (IUCN 1980). The trade in reptiles includes skins, organs, body fluids, and a large demand for many reptile species as pets (Jester et al. 1990). At least 1-2 million live snakes and lizards are sold internationally every year (Hemley 1994).

As is the case with most commodities, the United States is a net importer of pet reptiles. A review of CITES records reveals that the U.S. is the primary importer of live reptiles regulated under the treaty, with net imports of about twice as many animals as all European countries combined (Groombridge 1992). Other important importers include Austria, France, Japan, and Germany. The main exporters of these animals are tropical countries, primarily Honduras and Togo, followed by Surinam, Ghana, Madagascar, Malaysia, and the Philippines (Groombridge 1992).

Worldwide and domestically, trade in wildlife and wildlife products seems to be increasing despite rising concerns about the conservation of biodiversity (Wilkinson 1996, Malik et al. 1997). Trade in live reptiles in particular appears to be growing as the trade in live birds diminishes (Hoser 1992, Hemley 1994). Over the last few years, snakes have come to dominate the illegal portion of the pet trade (Webster 1997).

The desire of many Americans to have pet reptiles is partially satiated by a thriving legal and illegal domestic trade in native herpetofauna. The U.S. also exports reptiles in significant quantities for the pet trade, primarily to Europe and Japan. Several sources report that the illegal take of U.S. reptiles for the pet trade is at an all-time high and continues to increase (e.g., Potten 1991, Van Biema 1994, Wilkinson 1996). Rattlesnakes in particular are in high demand (Fitzgerald 1989).

The state of Arizona has attempted to stem the overexploitation of reptiles by taking bold steps prohibiting the sale of almost all native live animals and the collecting of some species with limited distributions (AGFD 1999). The collection of *C. pricei* without a scientific collecting permit has been prohibited in Arizona since the late 1960's. Twin-spotted rattlesnakes are also protected in Mexico (Mahaney 1997b).

At the international level, trade in rare reptiles and other animals is regulated by CITES. Federally, there are two laws that deal with reptile exploitation - the Endangered Species Act and the Lacey Act. Of these laws, only the Lacey Act applies to *Crotalus pricei*. This act, passed by Congress in 1900 and amended in 1981, prohibits the transport of illegally collected wildlife across state or international borders.

EVOLUTIONARY HISTORY

The original center of dispersal for rattlesnakes is believed to have been the north-central portion of Mexico's Central Plateau (Gloyd 1940, Smith 1946). The twin-spotted rattlesnake is thought to be one of the most primitive rattlesnake species evolutionarily, probably first arising in that area less than 24 million years ago during the Miocene and Pliocene epochs, and dispersing to the north into Arizona during the Pleistocene (Gloyd 1940, McCranie and Wilson 1987). As the climate grew warmer and drier at the end of the Pleistocene, *C. pricei* was forced to seek suitable microclimates at high elevations (Ernst 1992). As a result, in Arizona *C. pricei* became isolated in disjunct mountain ranges. These populations do not interbreed and may differentiate ultimately into separate subspecies and species, barring a major shift toward a cooler and wetter climate regime. Therefore, conservation of each population is particularly important.

Crotalus pricei is currently divided into two subspecies. *Crotalus pricei pricei*, the western twin-spotted rattlesnake, was described by Van Denburgh in 1895. This subspecies ranges from southeastern Arizona south along the Sierra Madre Occidental through eastern Sonora, western Chihuahua, and Durango, Mexico (Armstrong and Murphy 1979). A disjunct population that may belong to this subspecies is also known from Aguascalientes by one specimen (Campbell and Lamar 1989).

The other subspecies, *Crotalus pricei miquihuanas,* the eastern twin-spotted rattlesnake, was first described by Gloyd in 1940 and is located in the Sierra Madre Oriental in Coahuila, Nuevo Leon, and Tamaulipas, Mexico (Armstrong and Murphy 1979). The Mexican Plateau serves as a barrier to movement between the Sierra Madre Oriental and Sierra Madre Occidental, ensuring that no interbreeding presently can occur between the two subspecies.

DISTRIBUTION WITHIN ARIZONA

In Arizona, *Crotalus pricei* inhabit the Chiricahua, Huachuca, Santa Rita, and Pinaleño mountains . The species may be more abundant in the Chiricahuas than in the other ranges (Kauffeld 1957, Ernst 1992). *C. pricei* is also known from the Dos Cabezas Mountains from one record (Johnson and Mills 1982). Additional surveys are needed in the range for verification. A *C. pricei* specimen reportedly captured in the foothills of the Santa Catalina Mountains is in the Harvard University museum collection. This locality is almost certainly in error, as the Santa Catalinas are a highly visited range and no other *C. pricei* have been discovered there. Early reports of *C. pricei* in the Santa Catalinas (e.g., Van Denburgh 1922, Klauber 1936) are probably based on this erroneous specimen tag.

C. pricei is usually associated with rocky slopes (especially talus), ridges, and occasionally canyon bottoms between 1,860 m (6,100 feet) and 3,050 m (10,000 feet) (Van Denburgh 1922, Lowe 1964). *C. pricei* inhabits higher elevations than any other rattlesnake in Arizona. However, in some areas, populations of the species are sympatric with the rock rattlesnake (*Crotalus lepidus*), ridgenosed rattlesnake (*Crotalus willardi*), and blacktail rattlesnake (*Crotalus molossus*). In Arizona, the biotic communities associated with *C. pricei* are Madrean Montane Conifer Forest and Madrean Evergreen Woodland (Brown 1994).

POTENTIAL THREATS

Most of the *C. pricei* populations in Arizona occur on land managed by the U.S. Forest Service (USFS). Smaller populations may inhabit National Park Service and Bureau of Land Management areas. Potential threats to *C. pricei* populations in Arizona include mining, logging, grazing, recreational and other development, climate change, and collecting.

Large-scale mining, grazing, and logging are not anticipated in the near future within the range of *C. pricei*. Some herpetologists have suggested that recreational developments in the mountains of southeastern Arizona have negatively impacted the habitat of montane rattlesnakes, although data from those locations are lacking (Rubio 1992). Catastrophic fire may also have a negative impact on some montane rattlesnake populations, but the effect on *C. pricei* is unknown (A. Holycross, pers. comm.).

Global warming could cause problems for *C. pricei* in Arizona, as the species only inhabits the highest elevations within its range. A warming trend could further reduce the amount of suitable habitat for the species, potentially reducing population sizes and increasing the probability of extirpation due to stochastic events.

However, collection for the black market pet trade and associated habitat destruction is the primary threat currently faced by *C. pricei* (Johnson and Mills 1982). Recently, the Mt. Graham observatory was constructed in potential *C. pricei* habitat in the Pinaleño Mountains, and although construction was not anticipated to affect *C. pricei*, it has been suggested that increased visitation to the site could elevate collection pressure in the area (USFS 1986). There is evidence indicating that providing recreational access to areas inhabited by reptiles with market value can devastate those reptile populations (Williams 1999). Most collecting that occurs is illegal, although some *C. pricei* are collected under permit for zoos or scientific studies. As snakes become increasingly popular as pets, pressure on *C. pricei* in Arizona will likely become more severe.

STUDY OBJECTIVES

Little has been published regarding the ecology of *C. pricei*, and no information is available about population size or density, level of collecting pressure, or effects of collecting on *C. pricei* populations. The absence of this kind of information plagues snake conservation efforts worldwide (Dodd 1993). A report for the U.S. Fish & Wildlife Service highlighted the need for natural history information about *C. pricei* to answer management questions (Johnson and Mills 1982). This study was designed to address this need for information about the basic ecology, current status, and threats faced by this narrowly distributed and secretive species. Specifically, our objectives were to:

1. Quantify current and past hunting pressure of study sites based on habitat disturbance, historical information, and observations of present human activity.

2. Estimate population size and density through mark-resighting methods.

3. Determine age structure, sex ratios, growth rates, and survival through repeated measures of individual snakes.

4. Determine differences in movement, activity patterns, and behavior using radiotelemetry.

5. Examine relationship between distribution, abundance, and age structure of mountain spiny lizard populations and rattlesnake collecting.

6. Determine distribution of twin-spotted rattlesnakes within a one-mile radius of Barfoot Park and establish monitoring protocols for these populations based on repeatable methodology.

We attempted to accomplish these objectives by comparing a *C. pricei* population at a site reported to be under intense pressure from collectors with three sites in the same mountain range that are under little or no collecting pressure.

STUDY AREA

The Chiricahua Mountains are located near the southeastern corner of Arizona in Cochise County. The Chiricahuas, oriented roughly north-south, are bordered on the west by Sulphur Springs Valley and on the east by San Simon Valley. The range reaches a maximum elevation of 2,986 m (9,796 feet) and covers 152,300 ha (607 sq. mi.), making the Chiricahuas the second highest mountain range in southern Arizona and the largest in area.

The Chiricahua Mountains receive a bimodal precipitation distribution. In Chiricahua National Monument, 51.8% of the precipitation falls between July and September and 40.8% falls between October and March (National Weather Service 1999). Rustler Park Ranger Station, located near the study sites at 2,560 m (8,400 feet), receives an average of 760 mm (29.9 inches) of precipitation per year (Bennett et al. 1996).

The most well-known locality for twin-spotted rattlesnakes anywhere in their range is in the Chiricahuas at Barfoot Park, Coronado National Forest. Barfoot Park has been publicized as a locality for the species by natural history guides (e.g., Klauber 1972, Lowe et al. 1986) and snake collecting books (e.g., Kauffeld 1957, Kauffeld 1969). The snakes at this site served as the "hunted" population.

The Barfoot talus slopes are just north of Barfoot Park at an elevation of approximately 2,530 m (8,300 feet), and are composed of fragments of dacite, a volcanic rock (Du Bray et al. 1992). We focused our efforts primarily on two large, adjoining, south-facing talus slopes next to the road. Based on our observations, we believe that these two slopes, covering 3.1 ha (7.7 acres), attract most of the *C. pricei* collectors.

Barfoot and the other three study sites are in the Madrean Montane Conifer Forest vegetation association (Brown 1994). The most abundant plant species around the Barfoot slope edges are Gambel oak (*Quercus gambelii*), ponderosa pine (*Pinus ponderosa*), New Mexico locust (*Robinia neomexicana)*, and tasselflower (*Brickellia grandiflora)*.

Snake hunting is infrequent or nonexistent at the three control sites (Sites 1, 2, and 3), all located within 20 km of Barfoot Park. These sites were selected by investigating unvegetated areas marked on topographic maps (1:24,000) and visible in aerial photographs. Talus slides composed of rocks that appeared to be predominantly much larger or smaller than the rocks at Barfoot were excluded, as were slides visible from roads. Sites at which twin-spotted rattlesnakes were actually observed were selected as study sites.

Site 1 is a south and east-facing rhyolite talus slide that is similar to the Barfoot slide in size, at an elevation of about 2,900 m (9,500 feet). Four adjoining talus slopes were selected as the main study area, covering 3.3 ha (8.0 acres). The area around Site 1 was burned severely during the aptly-named Rattlesnake Fire of 1994. Numerous plant species have become well-established around the talus since that time, including quaking aspen (*Populus tremuloides)*, which dominates the area, many-flowered viguiera (*Heliodermis multiflora*), and tasselflower.

Site 2 is a west-facing dacite talus slide that is smaller than the Barfoot slide at an elevation of about 2,700 m (8,900 feet). Our efforts were concentrated on four adjacent talus slopes that covered 1.0 ha (2.6 acres). Dominant plant species are quaking aspen and Douglas fir (*Pseudotsuga menziesii*). Site 3 is another west-facing dacite talus slide, significantly smaller in area than the Barfoot slide, located at about 2,600 m (8,600 feet). The slide is composed of a single talus slope covering 0.7 ha (1.7 acres). The talus is surrounded predominantly by Douglas fir, quaking aspen, Gambel oak, mountain spray (*Holodiscus dumosus*), and tasselflower.

DURATION OF STUDY

Field work was conducted between June 1997 and October 1998. Montane rattlesnakes are most commonly observed during the summer monsoon season (Lowe et al. 1986). Our efforts were concentrated during this season and early fall, from July to mid-October.

ECOLOGY

METHODS

POPULATION SIZE AND DENSITY

Crotalus pricei were captured by hand using welding gloves or forceps. Snakes were marked uniquely with Passive Integrated Transponders (PIT tags) (Destron-Fearing Corp., South St. Paul, MN). In addition, up to three rattle segments of each snake were painted with a unique color code to enable visual identification of individuals.

Searches involved traversing talus, primarily during daylight hours. During searches, we spent about 70% of our time within 5 m of the edge of talus slopes, and most of the remainder on talus further from the edge. We also captured snakes opportunistically while conducting activities other than formal searches, such as radiotelemetry. The time spent walking on the talus while involved in these other activities was tallied as 50% search time.

We spent 144.9 person-hours searching for snakes at Barfoot in 1997 and 205.4 in 1998. At Site 1, we searched for snakes for 70.1 person-hours in 1997 and 109.6 in 1998. At Site 2, the number of person-hours for each year was 81.3 and 71.5, respectively. Finally, at Site 3, we spent 29.0 person-hours searching in 1997 and 25.1 in 1998.

During "roundups" held 24-27 July 1997 and 13-16 August 1998, we organized numerous volunteers to assist us in catching snakes at Barfoot, the major reason that search time at Barfoot was much greater than at the other sites. In 1997, 14 searchers spent 85.9 person-hours searching the two primary Barfoot slopes for snakes during the roundup. During the 1998 roundup, 21 searchers spent 79.1 person-hours on those slopes. Only a few volunteers were admitted to Sites 1, 2, and 3 during the course of the study due to our desire not to publicize other *C. pricei* localities. The amount of search effort at each site was also related to the size of the study area.

For analysis, person-hours at each site were divided into capture periods of equal search effort. At Barfoot, each capture period was approximately equal to the number of person-hours in the 1997 roundup (during which there were no previously marked animals). This resulted in a total of four capture periods of 87.6 person-hours per period.

Search effort was less at the other sites, so we used different search period lengths than those used to analyze the Barfoot data. At Site 1 and Site 2, each search period consisted of approximately 20 person-hours, resulting in nine and eight search periods for each site, respectively. At Site 3, about 10 person-hours made up a search period, resulting in five search periods.

Our radiotelemetry data indicated that snakes move off the talus slopes occasionally, meaning that the study areas did not constitute closed populations. Therefore, we analyzed our data by using the Jolly-Seber model in Program MARK, which is designed to estimate abundance in open populations (Jolly 1965, Seber 1965, White 1999). This model assumes equal catchability and survival probabilities among the study animals.

For comparison, we also used the Lincoln-Petersen model to estimate abundance by designating each year as a separate capture period. The Lincoln-Petersen model is a simple equation designed to work in closed populations where all animals are equally catchable at all times (see Lancia et al. 1996).

Finally, we calculated an index of *C. pricei* population density for each site by dividing the number of animals captured or observed by the number of search hours. For comparative purposes, indices rely on equal observability at all times, and in our study observability fluctuated with weather conditions and time of year. However, we believe that we spent enough time at each site for any differences to affect all sites more or less equally. Unlike the previous two methods, an index allows us to include snakes that were never captured, which helps eliminate the effect of variability of snake-catching abilities among different workers.

MORPHOLOGY

We measured snout-vent length (SVL), mass, and other morphological characteristics of all snakes captured. Snakes captured outside, but near, study sites were included in the analyses. One randomly selected capture event was analyzed for snakes captured more than once, but only data from the initial capture was used for radiotelemetered snakes. Sex was determined by cloacal probing, and many snakes were palpated to determine the presence of embryos or food boli.

JMP IN 3.2.1 (SAS Institute, Inc.) was used to perform statistical analyses. SVL and mass were compared using analysis of variance (ANOVA). Mass was analyzed after a natural log transformation. Sex and age class were compared using contingency tables and Pearson chi-square tests.

To examine differences between hunted and unhunted populations, data from the three unhunted sites were pooled and compared with the Barfoot data. Snakes at south-facing and west-facing sites were compared to determine if aspect is likely to affect demographics. Also, snakes at Barfoot and Site 1, the site most similar to Barfoot in size and aspect, were compared. The ratio of tail length: total length, a measure often used to determine the sex of rattlesnakes, was estimated for each sex. A regression line was developed to express the length-mass relationship for the species to compare *C. pricei* with other montane rattlesnakes.

The smallest gravid *C. pricei* reported by Klauber (1972) measured 301 mm total length. No information has been published regarding the size at which male *C. pricei* become reproductively active. Therefore, snakes smaller than 301 mm were considered to be juveniles in analyses.

GROWTH

Mean growth rates (SVL and mass) were calculated from recapture data. A Student's t-test was performed to determine if these rates differed from zero. Differences between sites, sexes, radiotelemetered vs. non-radiotelemetered animals, and sizes were assessed using ANOVA.

SURVIVAL

The Jolly-Seber model in Program MARK was used to estimate the average survival rate of snakes at each site (Jolly 1965, Seber 1965). Due to the small sample sizes, it was not possible to differentiate between juveniles and adults in the analysis. Each site was analyzed separately using the same capture periods described previously.

DIET

Fecal samples were obtained when snakes defecated while held individually for a short time in plastic containers prior to processing. No other form of encouragement was used to obtain samples. Fecal samples were placed in Whirlpak plastic bags with 70% isopropyl alcohol. In the lab, samples were cleaned by the addition of more alcohol and agitation before being separated into pieces either with forceps and needles or with a jet of distilled water and a fine sieve. Prey were identified by using a light microscope to compare samples with specimens of animals known to occur in the area.

REPRODUCTION

Data obtained from snake palpation, the radiotelemetry portion of the study, and other observations were used to speculate about the reproductive cycle of *C. pricei* in the Chiricahuas. Differences between gravid and non-gravid snakes were assessed with ANOVA. Two snakes involved in the radiotelemetry study were not identified as being gravid through palpation, but are believed to have been gravid based on behavioral observations. These two snakes are not included in the gravid category for the statistical tests. Details regarding a clutch of neonates and the first reported field observation of mating *C. pricei*, as well as observations of male/female pairs, are also reported.

HABITAT

At each snake capture and observation site, we recorded numerous habitat variables, including the dominant vegetation type within 5 m, nearest vegetation type, distance to nearest vegetation, and distance to edge of talus slope. Habitat variables from radiotelemetered and non-radiotelemetered snake locations were pooled for analysis. At Barfoot, we also collected habitat data at 50 random points on the largest talus slope. To determine whether snakes were selecting certain habitat features, 112 habitat points for snakes on this slope were compared with the randomly placed points.

RADIOTELEMETRY AND ACTIVITY PATTERNS

We surgically implanted temperature-sensitive radiotransmitters with whip antennas into 16 snakes (Holohil Systems, Ltd., Carp, Ontario, Canada). We primarily used 1.8 g transmitters with an expected battery life of four months ($n = 13$), but also used 3.3 g transmitters designed to last for six months ($n = 3$). Some surgeries were performed in the field and others in the lab.

To anaesthetize the snakes, a hollow plastic tube was connected to a plastic container which held 2-3 gauze pads and connected to a bag-valve pump. The anterior portion of the snake was placed in the tube and 1-3 ml of Isoflurane was applied to the gauze pads. The resulting gas was pumped into the tube until the snake lost consciousness. For surgery, sterile surgical gloves were worn, all surgical instruments were sterilized by autoclave, radiotransmitters were gas sterilized, and the operation was performed on a sterile towel.

The snake's skin was scrubbed three times at the incision site with a betadine solution and rinsed. An incision was made about 1/3 of the way from the posterior end of the snake between the dorsal and ventral scales, and the transmitter was placed gently into the abdominal cavity. The length of the antenna was measured along the body of the snake anterior to the transmitter location, and a small incision was made in the snake's skin near the antenna's end. The antenna was then fed into a narrow catheter, and the catheter was tunneled subcutaneously from the transmitter site to the anterior incision. The catheter was pulled out of this second incision, leaving the antenna under the snake's skin. Synthetic absorbable Lactomer Polysorb 4.0 suture was used to close the peritoneal wall, and the skin was stitched with nylon Monosof 3.0 suture. Fresh air was pumped into the tube as the final stitches were sewn. Snakes were usually held and observed for at least 24 hours after surgery.

Snakes were selected from Barfoot, Site 1, and Site 2 for the radiotelemetry portion of the project. In addition to excluding snakes for which the radiotransmitter was equal to more than 5% of the body weight of the animal, some snakes were rejected because they appeared to be too thin to accommodate the transmitter.

In 1997, we placed transmitters in nine snakes, including five males and one female at Barfoot, one male and one female at Site 1, and one male at Site 2. In 1998, we followed ten snakes, including three males and three females at Barfoot, one male and two females at Site 1, and one male at Site 2.

We replaced transmitters in three of these snakes to collect data on single individuals over a longer period of time than four months. The male at Site 2 was followed for the longest amount of time, from 9 August 1997 to 8 September 1998. One female at Barfoot was tracked from 24 July 1997 to 19 May 1998, and a male at Barfoot was followed from 16 September 1997 to 13 January 1998, and then again from 8 July to 27 September 1998.

A TR-4 receiver (Telonics, Inc., Mesa, AZ) and two-element flexible Yagi antenna were used to locate snakes. Snakes were located once a week between July and mid-October, and once a month during other times of the year. We also observed five snakes intensively, which involved watching an animal constantly for two-hour periods, separated by two-hour breaks, over the course of one or two days. During these periods, weather conditions and body temperatures were recorded every 30 minutes. The snakes were also relocated every 30 minutes if not already visible.

Distances between snake locations were measured with a tape measure and/or Bushnell rangefinder, and a Suunto compass and clinometer. Pitter Plotter 1.2 (Concentrics Co.), a cave mapping program, was used to determine the true distances between points. Home range size was estimated with Calhome (Pacific Southwest Research Station, USFS), using the 100% minimum convex polygon model. Differences in distance moved per week, home range size, and proportion of observations on talus were compared.

The number of snakes involved in the study varied over time. The largest number of snakes were tracked between July and September of each year. Comparisons therefore only involve observations made during those months unless otherwise stated.

RESULTS

We marked a total of 109 *C. pricei* during the two-year study, including 65 snakes at Barfoot, 44 at unhunted sites, 92 on south-facing slopes (Barfoot and Site 1), 17 on west-facing slopes (Sites 2 and 3), and 27 at Site 1.

POPULATION SIZE AND DENSITY

Only snakes captured within formal study areas (n = 92) were included in the population size and density analyses. Abundance and density estimates are summarized in Table 1. The estimates suggest that Barfoot has the highest abundance and encounter frequency. The Lincoln-Peterson formula could not be used for the Site 2 population because no 1997 snakes were recaptured in 1998. Program MARK could not be used for the Site 3 population, presumably due to low sample size.

Table 1. Twin-spotted rattlesnake abundance and density estimates

	Snakes Marked	No. of Recaps	MARK Abundance			Lincoln-Petersen Abundance	MARK Density (snakes/ ha)	Lincoln-Petersen Density (snakes / ha)	Density Index (snakes/ search hour)
			n	SE	95% CI				
Barfoot	48	24	95.8	41.2	47.4 to 224.3	88.9	30.6	28.4	0.31
Site 1	27	8	54.2	31.8	20.4 to 161.4	60.0	16.7	18.5	0.22
Site 2	12	1	87.1	91.9	17.8 to 481.1	-----	83.8	-----	0.14
Site 3	5	1	-----	-----	-----	9	-----	13.0	0.20

Although the high encounter rate at Barfoot suggests a higher snake density at Barfoot than other sites, the difference is not important statistically (F = 5.63, df = 2, 2, *P* = 0.14) (Table 2). There was no apparent density difference between south-facing and west-facing slopes (F = 3.11, df = 2, 2, *P* = 0.22).

Table 2. Twin-spotted rattlesnake density indices

	Snakes/ Search Hour	Standard Error
Barfoot	0.311	-----
Unhunted Sites	0.188	0.026
South-Facing Sites	0.267	0.044
West-Facing Sites	0.170	0.033

SIZE

Snout-vent length (SVL) for all 109 *C. pricei* captured averaged 389.2 mm (SE = 9.05, 95% CI = 371.2 to 407.1, range = 176 to 572). The largest snake for which sex could not be ascertained measured 301 mm. If snakes 301 mm and smaller are excluded from the analysis, males and females do not differ in SVL (diff. = 7.02 ± 14.38 mm, F = 0.24, df = 2, 87, *P* = 0.63). However, only males were larger than 540 mm.

Average SVL was 38.1 mm greater at unhunted sites than at Barfoot (SE = 18.2, 95% CI = 2.1 to 74.1, F = 4.4, df = 2, 107, $P = 0.038$) (Figure 1; Table 3). Snakes on west-facing slopes tended to be larger than those on south-facing slopes, although there was no difference statistically (diff. = 40.8 ± 24.7 mm, F = 2.73, df = 2, 107, $P = 0.10$). There was also no statistical difference between Barfoot and Site 1, although on average the Site 1 snakes were larger (diff. = 30.7 ± 20.9 mm, F = 2.15, df = 2, 90, $P = 0.15$).

Table 3. SVL and mass comparisons

	SVL (mm)	SE	MASS (g)	SE
All	389.2	9.1	53.8	3.6
Barfoot	373.8	11.8	47.8	4.8
Unhunted	411.9	13.5	62.6	5.2
South-facing	382.8	9.6	50.9	3.8
West-facing	423.6	25.1	69.3	9.3
Site 1	404.5	15.7	58.4	6.2

Mass of all snakes captured averaged 53.8 g (SE = 3.6, 95% CI = 46.7 to 60.9, range = 3.6 to 188.5). Male and female snakes above 301 mm SVL did not differ on average (66.6 ± 5.8 vs. 59.3 ± 3.8 g, ln-transformed: F = 0.0014, df = 2, 87, $P = 0.97$). However, only male snakes exceeded 115 g.

On average, snakes at unhunted sites were 1.36 times heavier than Barfoot snakes (SE = 1.16 times, 95% CI = 1.04 to 1.68 times, ln-transformed: F = 5.06, df = 2, 107, $P = 0.027$). Slope aspect did not significantly affect mass (diff. = 1.33 ± 1.22 times, ln-transformed: F = 2.34, df = 2, 107, $P = 0.13$). Site 1 snakes tended to be heavier than Barfoot snakes (diff. = 1.32 ± 1.19 times, ln-transformed: F = 2.90, df = 2, 90, $P = 0.092$).

The ratio of tail length: total length differed substantially between the sexes (F = 176, df = 2, 96, $P < 0.0001$). The male ratio averaged 0.0863 (SE = 0.00086, 95% CI = 0.0846 to 0.0880); the female ratio was 0.0687 (SE = 0.001, 95% CI = 0.0667 to 0.0707). However, there was some overlap (male range = 0.0656 to 0.0994, female range = 0.0429 to 0.0816).

SEX AND AGE

Sex could not be determined for 11 of the 109 snakes captured due to their small size. Overall, 59.2% of the snakes for which sex could be determined were males, and there is some evidence that the population differed from a 50:50 sex ratio ($\chi^2 = 3.31$, df = 96, $P = 0.069$). There was no difference in sex ratio between Barfoot and unhunted sites (59.6%

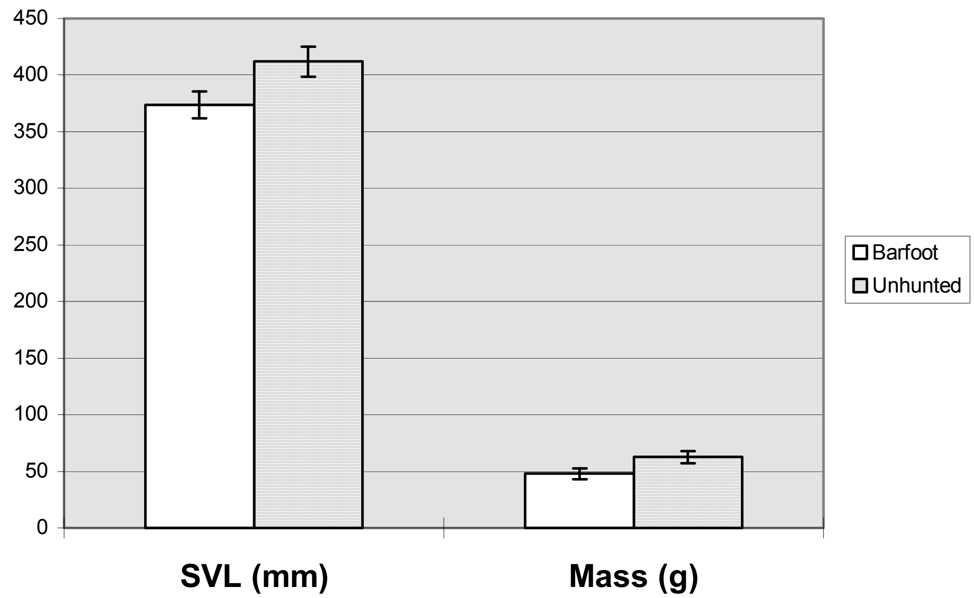

Figure 1. SVL and mass comparison: Barfoot (n = 65) vs. unhunted sites (n = 44)

vs. 58.5% male, χ^2 = 0.012, df = 96, *P* = 0.9120). Sex ratio also did not differ between south and west-facing slopes (60.2% vs. 53.3% male, χ^2 = 0.251, df = 96, *P* = 0.6164) or between Barfoot and Site 1 (59.6% vs. 61.5% male, χ^2 = 0.027, df = 81, *P* = 0.8704).

Eighty-six percent of all snakes captured were adults. There was no difference in adult: juvenile ratio between Barfoot and unhunted sites (83% vs. 91% adult, χ^2 = 1.36, df = 107, *P* = 0.24). This ratio had no relation to aspect (86% (south) vs. 88% (west) adult, χ^2 = 0.068, df = 107, *P* = 0.79) and Barfoot and Site 1 were similar (83% vs. 93% adult, χ^2 = 1.42, df = 90, *P* = 0.23).

If we assume that SVL is directly related to age, a comparison of SVL histograms reveals that the Barfoot population has a relatively normal age distribution, whereas that of the unhunted sites is skewed low (Figure 2). Relatively large numbers of Barfoot snakes were between 200 and 250 mm SVL and between 300 and 350 mm, whereas few snakes were between 450 and 500 mm at Barfoot compared to unhunted sites.

GROWTH

During the course of the study there were 51 recapture events, including radiotelemetered animals. On average, these snakes grew 0.150 mm SVL/ day between recaptures (SE = 0.062, 95% CI = 0.0250 to 0.275). This growth rate differed significantly from zero (t = 2.41, df = 50, *P* = 0.020). Snakes at the hunted site (n = 38) tended to grow slightly faster than snakes at unhunted sites (n = 13), but the difference was not substantial (diff. = 0.218 ± 0.141 mm/ day, F = 2.41, df = 2, 49, *P* = 0.13). There was no difference in growth rates between male (n = 24) and female (n = 25) snakes (diff. = 0.102 ± 0.130 mm/ day, F = 0.61, df = 2, 47, *P* = 0.44).

The smallest radiotelemetered snake measured 430 mm SVL when initially captured. Snakes smaller than 430 mm (n = 23) grew at a substantially faster rate than snakes 430 mm and larger (n = 28) (diff. = 0.347 ± 0.116 mm/ day, F = 8.93, df = 2, 49, *P* = 0.0044). The growth rates of snakes 430 mm and larger were not affected by the radiotransmitters (diff. = 0.097 ± 0.125 mm/ day, F = 0.60, df = 2, 26, *P* = 0.45).

On average, snakes lost mass between recapture events (-0.043 ± 0.0373 g/ day, 95% CI = -0.118 to 0.0321), but this rate was not statistically different from zero (t = -1.15, df = 50, *P* = 0.26). There was no difference in mass change between snakes at hunted and unhunted sites (diff. = 0.0381 ± 0.0856 g/ day, F = 0.20, df = 2, 48, *P* = 0.66). Male and female snakes did not differ in weight change (diff. = 0.045 ± 0.078 g/ day, F = 0.33, df = 2, 46, *P* = 0.57).

Snakes smaller than 430 mm SVL tended to gain mass; larger snakes tended to lose mass (diff. = 0.184 ± 0.0707 g/ day, F = 6.75, df = 2, 48, *P* = 0.012). The presence of radiotransmitters did not greatly affect weight gain or loss (diff. = 0.129 ± 0.112 g/ day, F = 1.32, df = 2, 25, *P* = 0.26). The difference between snakes with and without

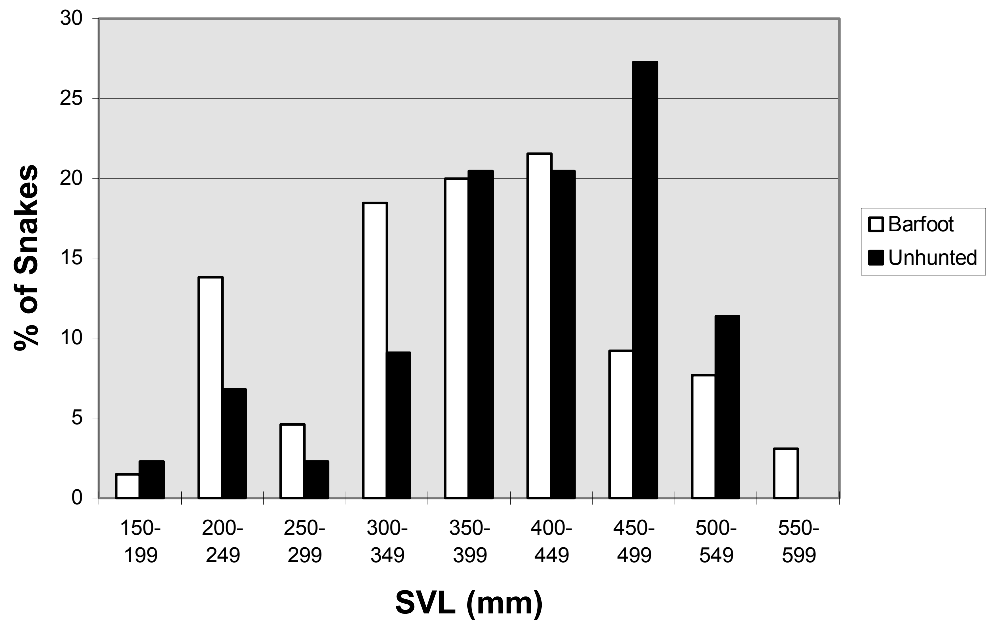

Figure 2. Size distribution comparison: Barfoot (n = 65) vs. unhunted sites (n = 44)

radiotransmitters was almost nonexistent when snakes that lost weight due to parturition were excluded (diff. = 0.031 ± 0.061 g/ day, F = 0.263, df = 2, 22, *P* = 0.61).

The length-mass relationship for *C. pricei* is: $\log_{10}$ mass = -6.209 + 3.033 $\log_{10}$ SVL (F = 1780, df = 2, 107, *P* = 0.0001, R^2 = 0.9433).

SURVIVAL ESTIMATES

The survival rate between capture periods at Barfoot was 0.905 (SE = 0.212, 95% CI = 0.071 to 0.999). A slightly higher survival rate was estimated for Site 1 of 0.953 (SE = 0.135, 95% CI = 0.055 to 1.000). Reasonable estimates were not produced for Sites 2 or 3, probably due to the small sample sizes at those sites.

DIET

Snakes were palpated for food boli on 91 occasions. Food boli were detected in 33% of these snakes, including 42% of the males (n = 45) and 19% of the females (n = 43), a substantial sex difference (χ^2 = 5.77, df = 86, *P* = 0.016).

Snakes checked in April to June 1998 (n = 6) did not have food boli. Percentages of snakes with food boli during July-September 1998 are illustrated in Figure 3. Males were more likely to have food boli than females during those months, with the largest difference in August. Food was detected in both snakes captured in October 1998.

Site 1 had the lowest percentage of snakes with food boli (n = 19), with 21% of assessed snakes containing food, or 27% if snakes examined before July are excluded. There was no difference between Barfoot (n = 62) and the unhunted sites (n = 29) (32% vs. 34% with food boli, χ^2 = 0.044, df = 89, *P* = 0.83).

Twenty-eight fecal samples were collected and analyzed, 26 of which contained identifiable prey items (Figure 4). Lizard scales were found in 20 (71.4%) of the samples. All of the scales are from *Sceloporus*, and at least eight samples contain mountain spiny lizard (*Sceloporus jarrovii*) scales. The lizard species could not be determined for the other twelve samples, but most are probably also *S. jarrovii*.

One fecal sample contained snake scales and a rattle. The rattle size and shape and the coloration of the scales matched most closely with specimens of *C. pricei*. The rattle consisted of one segment and a button. A comparison of the ventral scales in the sample with *C. pricei* specimens suggests that the prey snake measured approximately 225 mm SVL. According to our length-mass curve, a snake of this size would weigh about 8.4 g. This sample was obtained on 28 September 1998 from a male snake measuring 466 mm SVL and weighing 70 g.

Hairs were found in five samples (17.9%). Bones in one of these samples were identified as *Peromyscus*, most likely a brush mouse (*P. boylei*), other mammal prey items were not

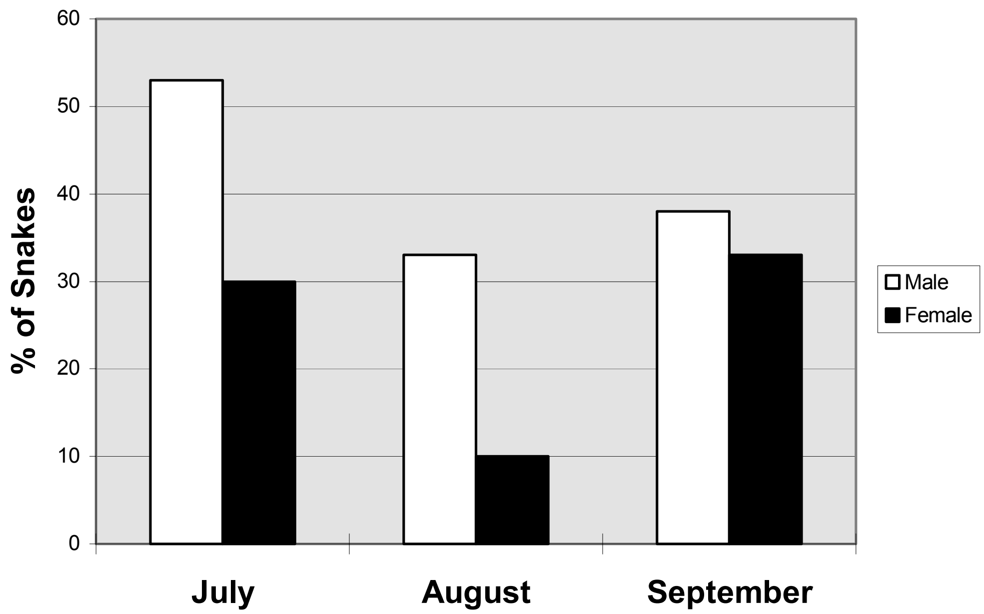

Figure 3. Percentage of snakes with food boli in 1998

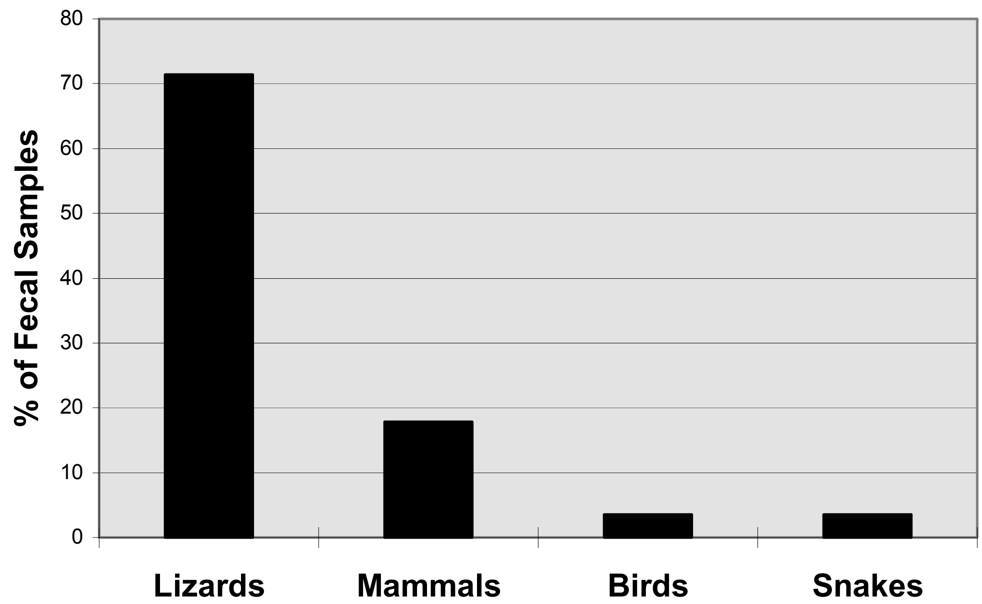

Figure 4. Prey distribution in twin-spotted rattlesnake fecal samples (n = 26)

identified. The smallest snake from which mammal remains were obtained measured 240 mm SVL and weighed 7.6 g. Mammal prey was found in samples taken between 8 July and 10 September.

Feathers were found in a sample obtained on 8 July 1998 from a male that measured 530 mm SVL and weighed 142 g. The color gradation of the feathers and the rachis color suggest the prey was a canyon wren (*Catherpes mexicanus*).

Eighty percent of the 19 samples obtained from snakes captured on talus contained *Sceloporus*, whereas 16% contained mammals. Off talus, *Sceloporus* accounted for 67% of the prey of the six snakes producing samples, with mammals making up the other 33%. Both the bird and *C. pricei* prey were obtained from snakes found on talus.

We observed one successful, unstaged feeding strike on the talus during the study. A small *C. pricei* (301 mm SVL, 12.5 g) struck a large *Sceloporus jarrovii* (149 mm total length, 10.2 g) on the head. The snake attempted to hold on to the lizard following the strike, but after about six minutes the lizard was able to free itself from the snake's grasp. The lizard became unable to turn itself over 16 minutes after the bite, and stopped breathing 10 minutes later.

REPRODUCTION

Twenty-eight adult female snakes were palpated for embryos, mostly in 1998. Embryos were detected in 13 (46.4%) of these snakes. During 1998, no embryos were detected before 9 June or after 20 August. The average number of embryos detected per gravid snake was 3.85 (SE = 0.458, 95% CI = 2.85 to 4.84, range = 1 to 6).

On average, gravid snakes measured 435 mm SVL (SE = 11.9, range = 364 to 500) whereas non-gravid snakes measured 425 mm (SE = 15.0, range = 316 to 534), indicating that adult SVL was not related to reproduction ($F = 0.28$, df = 2, 26, $P = 0.60$). The smallest gravid snake measured 364 mm SVL and weighed 32 g on 9 June; she appeared to have two embryos. On 10 August, the same snake weighed 40.5 g and still had the embryos.

Male and female snakes were observed in close proximity to each other (≈ one meter) on 13 occasions between 11 August and 21 September 1997 and between 9 August and 13 September 1998.

One mating event was observed during the study. Although courtship and copulation can be very similar in appearance, it appeared to us that the cloacas of the two snakes were connected during the event. A female snake and a radiotelemetered male were observed under a rock together near the edge of a large talus slope on 11 August 1997. The male measured 492 mm SVL and weighed 92.5 g on 27 July 1997; the female measured 466 mm SVL and weighed 64.5 g on 11 August 1997. The two snakes were observed in close proximity to each other again at the same location on 14 August. Mating was observed between these two snakes on 21 August. The snakes had moved off talus into a *Brickellia grandiflora*-dominated area about 6.5 m from their previous location.

At 0826 on 21 August, the male snake was observed chin-pressing and tongue flicking over the body of the female. At 0851, the tails of the two snakes became intertwined and copulation began. Over the next hour, their behavior was characterized by vigorous tail movement for about four seconds, followed by about 20 seconds of motionlessness, and then a return to chin-pressing and tongue-flicking by the male. This cycle was repeated approximately every three minutes. Copulation continued until 0949. The temperature profile about 3 m away from the snake location was: 1.5 m = 22.5°C, 0.5 cm = 24.0°C, substrate = 25.0°C. The body temperature of the male snake during copulation was 34°C. The same female snake was found carrying three or four embryos on 13 August 1998. At that time she measured 475 mm SVL and weighed 74.5 g.

A snake measuring 441 mm SVL and weighing 66.5 g gave birth to four neonates sometime between 2100 on 16 August and 1430 on 17 August 1998 while being held in a Tupperware container after processing. She had been captured on 16 August at 1418. Her mass after the birth was 42.5 g, indicating that the neonates and associated tissues comprised 36% of her body weight during pregnancy. On 20 August, the neonates averaged 168.8 mm SVL (SE = 2.32, range = 163 to 173) and 4.4 g (SE = 0.04, range = 4.3 to 4.5).

Three radiotelemetered females gave birth, although none of the neonates were observed. Only one gravid female was monitored for at least a few weeks before and after the date we believe she gave birth. A radiotransmitter was implanted into a 461 mm SVL, 89.8 g female with two detectable embryos on 10 July 1998. On 15 August, the snake still had the embryos and weighed 91.2 g. The snake remained within about a 4 meter radius (avg. movement = 3.2 m/ week) in a small island of vegetation on a large talus slope from her initial capture date (7 July) until 29 August. She was found 66 m away on 1 September. Between 29 August and 27 September she moved 39.9 m/ week on average. On 28 September she weighed 49 g, having lost 46% of her body mass since 15 August.

A 500 mm SVL, 92 g female with five wriggling embryos was implanted with a radiotransmitter on 16 August 1998. The snake was still in the original capture location on 20 August and had not yet given birth. By 25 August, she had moved about 9.5 m from her capture location, and by 29 August she had moved at least an additional 41 m. On 8 September, she was in close proximity to an adult male and was no longer carrying embryos. It is unknown when she actually gave birth. On 28 September, she weighed 53 g, having lost 42% of her body mass.

A 447 mm SVL, 71 g snake was captured on 20 May 1998 and given a radiotransmitter. No embryos were detected at that time. However, on 10 September she weighed only 48.5 g, having lost 32% of her weight. This suggests that she may have become pregnant, but embryo development had not begun in May. Between 20 May and 18 July, she moved 21.3 m/ week on average. After this early summer movement, the snake was always found within a one meter radius (avg. movement = 1.1 m/ week) between 18 July and 1 September. Then on 7 September she was found 134 m away from her previous location in close proximity to a male snake.

A fourth radiotelemetered female produced one non-viable embryo and four masses after an unsuccessful attempt to anaesthetize the snake in order to remove an expired transmitter on 4 September 1998. When first captured on 20 May, she measured 449 mm SVL and weighed 80.5 g; ova were detected. When recaptured on 1 September, she weighed only 73 g, indicating that embryo development over the summer had not been successful. However, her movement pattern was similar to that of the other gravid females. She moved over 60 m between her initial capture date and 11 July (avg. distance = 8.2 m/ week), and then remained practically stationary until recaptured on 1 September.

Neonate snakes were captured on 15 September 1997 (185 mm SVL, 3.6 g), 22 September 1997 (200 mm SVL, 7.1 g), and 30 September 1997 (176 mm SVL, 6.1 g). Neonates were found at all sites except Site 2.

HABITAT

Habitat data was collected at 375 *C. pricei* observation points. Most snakes that were on talus slopes were found near slope edges. The average distance from the edge for snakes on talus was 4.66 m (SE = 0.42, 95% CI = 3.84 to 5.48, range = 0 to 53). Most snakes were also found near vegetation (mean dist. = 1.23 m, SE = 0.13, 95% CI = 0.98 to 1.49, range = 0 to 19.1).

For snakes on talus, there was no difference between Barfoot and unhunted sites regarding distance from the talus edge (diff. = 0.14 ± 0.85 m, F = 0.25, df = 2, 277, $P = 0.87$). However, Barfoot snakes tended to be a little bit farther from vegetation than unhunted snakes (diff. = 0.87 ± 0.26 m, F = 11.0, df = 2, 372, $P = 0.001$).

The snakes on the largest Barfoot slope were much closer to the talus edge than randomly placed points (snakes: mean dist. = 4.94 ± 0.82 m, random: mean dist. = 22.39 ± 1.83 m, F = 101, df = 2, 148, $P < 0.0001$). Snakes were also closer to vegetation than random points (snakes: mean dist. = 1.73 ± 0.26 m, random: mean dist. = 10.10 ± 0.79 m, F = 163, df = 2, 160, $P < 0.0001$).

The most common dominant vegetative cover type within 5 m of our random points was no vegetation (76%), followed by *Brickellia grandiflora* (10%), and *Quercus gambelii* (8%). The dominant vegetative cover type around the snakes was usually *Quercus gambelii* (30%), followed by *Brickellia grandiflora* (26%), no vegetation (13%), and *Robinia neomexicana* (12%).

The closest plant species to most random points was *Brickellia grandiflora* (54%), followed by *Quercus gambelii* (26%) and *Symphoricarpos oreophilus* (10%). The nearest plant species to the snakes were *Brickellia grandiflora* (37%), *Quercus gambelii* (30%), *Robinia neomexicana* (7%), and *Symphoricarpos oreophilus* (5%).

Males observed by radiotelemetry exhibited differing affinities for talus during the monsoon months in each year. In 1997, four males were found on the talus 87.5% of the time (SE = 9.5, range = 60% to 100%), whereas in 1998, five males spent only 44.5% of their time on talus (SE = 13.6, range = 0% to 76.9%), indicating a substantial behavioral difference (F = 6.0, df = 2, 7, $P = 0.0442$).

Radiotelemetered females varied in talus use during suspected times of pregnancy in July and August. Three gravid females were found on talus 33%, 75%, and 100% of the time in 1998, whereas the non-gravid female was observed on talus 40% of the time during that period in 1997.

MOVEMENTS

Overall, males (n = 9) moved an average of 30.8 ± 20.4 m farther per week than females (n = 5) during the monsoon months (July to September), although the variance was high (male range: 2.63 to 115.44 m/ week, female range: 4.68 to 42.45 m/ week).

Movement patterns of gravid females (n = 3) were characterized by little movement (≤ 3.2 m/ week) between mid-July and the time we believe they gave birth at the end of August, followed by greatly increased movement following parturition in September (average: 73.1 ± 30.4 m/ week, range = 38.5 to 133.6 m/ week). In contrast, the non-gravid female moved 53.5 m/ week between 24 July 1997 and 29 August, and 30.0 m/ week between 29 August and 30 September. A comparison of the movement of gravid females during July and August (prior to their large movements which we believe signified the end of their pregnancy) with the non-gravid female during the same period reveals a large difference (diff. = 49.0 m/ week, SE = 1.34, F = 1329, df = 2, 2, P = 0.0008).

On average, males moved 73.8 ± 13.7 m/ week farther in 1998 than 1997 during the monsoon months.(F = 29.2, df = 2, 7, P = 0.001) (Figure 5). In 1997, males (n = 4) moved an average of 14.0 m/ week (SE = 6.2, 95% CI = -5.8 to 33.8, range = 2.6 to 30.2). Males generally stayed in the same location for a few weeks, then moved a short distance and remained in the new location for a period of time. In 1998, males (n = 5) moved 87.8 m/ week (SE = 11.0, 95% CI = 57.2 to 118.5, range = 64.9 to 115.4). These snakes were rarely in the same place on consecutive weeks.

One male was monitored over most of both monsoon seasons. He exhibited a strong difference in movement pattern between the years, moving almost four times as far per week in 1998 compared to 1997 (Figure 6).

Due to the apparently confounding effects of year and pregnancy, it is difficult to compare movements of snakes at hunted and unhunted sites. However, a comparison of males during the 1998 monsoon season indicates that males at Barfoot (n = 3) moved shorter

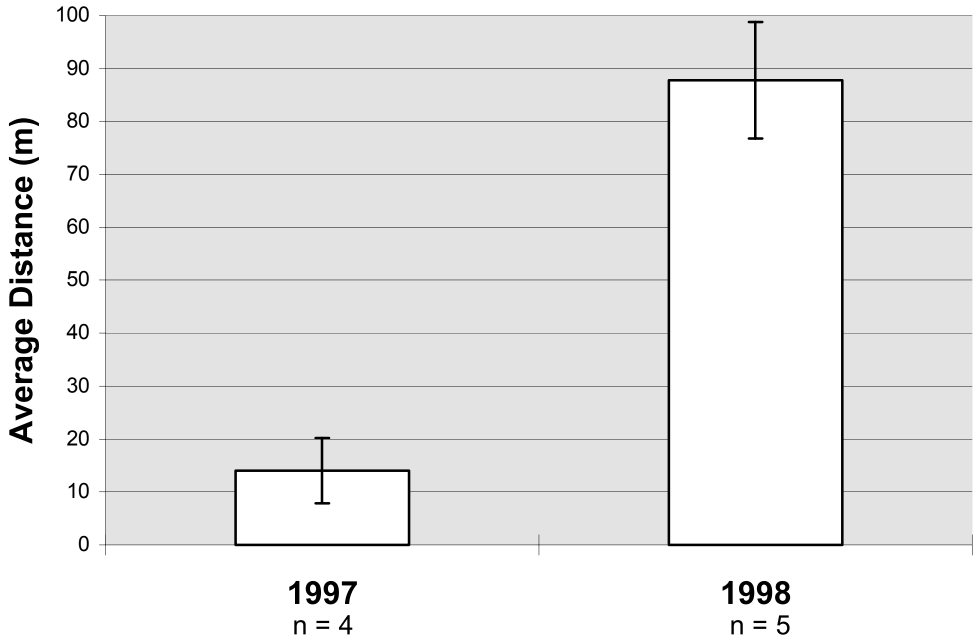

Figure 5. Male monsoonal movements: average distance moved per week

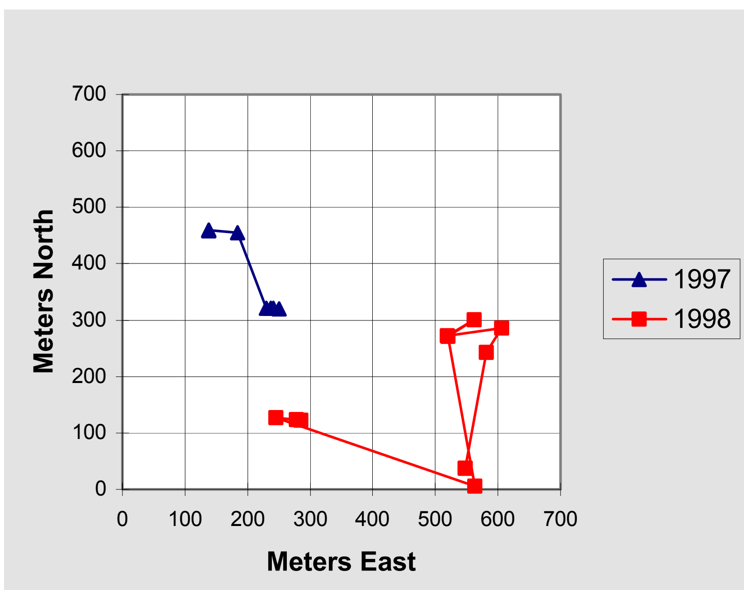

Figure 6. Monsoonal movements of a male twin-spotted rattlesnake

distances than males at unhunted sites (n = 2) (diff. = 44.1 m/ week, SE = 5.5, $F = 64.8$, df = 2, 3, $P = 0.004$).

HOME RANGE SIZES

The average home range size for males (n = 9) during the monsoon months (July to September) was 1.37 ha (SE = 0.60, 95% CI = -0.014 to 2.76, range = 0.0038 to 5.34). For females (n = 4) during the same period it was 0.36 ha (SE = 0.16, 95% CI = -0.14 to 0.86, range = 0.18 to 0.83). This difference was not important statistically (ln-transformed: $F = 0.033$, df = 2, 11, $P = 0.86$).

There was a large difference between home range size of males during monsoons in 1997 (n = 4) and 1998 (n = 5) (mean 1997: 0.16 ± 0.10 ha, mean 1998: 2.3 ± 0.88 ha, ln-transformed: $F = 12.0$, df = 2, 7, $P = 0.0104$). The home range of the male monitored during most of the monsoon seasons in both years was over 12 times larger in 1998 than in 1997. His home range over the entire 13 months he was followed was 14.7 ha. He did not revisit any of his 1997 locations in 1998, and his home ranges during the two monsoon seasons did not overlap.

The non-gravid female monitored in 1997 had a substantially larger home range size during the monsoon than the gravid females tracked in 1998 (non-gravid: 0.83 ha, gravid: 0.20 ± 0.011 ha, $F = 801$, df = 2, 2, $P = 0.0012$). Home range of one of the gravid females could not be calculated because her movements were too limited.

Barfoot males (n = 3) had smaller home ranges than males at unhunted slopes (n = 2) during the 1998 monsoon (diff. = 3.31 ha, SE = 0.78, $F = 18.1$, df = 2, 3, $P = 0.024$).

INTENSIVE OBSERVATION PERIODS

Three males and two gravid females were observed for blocks of time over a 24 to 36 hour period. Females were observed on cool, rainy days in July 1998. No nocturnal activity was detected for either snake. Females were observed basking in the late morning and early afternoon, even though cloud cover was always ≥ 90%. Heavy rain seemed to cause the snakes to retreat back under rocks, but they usually remained exposed during light rain.

Males were observed on relatively dry, sunny days in late August and early September. Two of the three snakes were seen above ground at night - one remained in a resting coil during the nocturnal observation period, the other was moving across the talus. None of the snakes were visible at 0700, but each came out to bask between 0800 and 0900. Average body temperature at 0700 was 15.2°C; by 0900 the average was 28.7°C. Daytime activity consisted of basking, moving short distances, and taking cover under rocks and logs. Snakes sought cover at body temperatures between 33.3° C and 34.3°C.

WINTER ACTIVITY

Three snakes were tracked over the winter of 1997-98. At least one snake was visible during monthly trips in November, December, January, and March (we were unable to access the area in February due to heavy snowfall).

In mid to late October 1997, the two males moved to new talus slopes where they spent the winter. The distances they moved to their winter locations were larger than any distances they had traveled previously. They selected locations near the edge of each slope where snowmelt was relatively rapid and that got quite warm occasionally during the winter. At one of these sites on 15 December 1997, the substrate temperature was 41.6°C (air temp. at 1.5 m = 15.6°C).

The female snake spent the winter off talus. Part of the time, she was in an area densely vegetated with ground cover (mostly *Eriogonum jamesii*). She may have concealed herself in the soil, or in a crack in a buried rock. The rest of the time, she was under a surface rock. Like the males, she moved into her winter area in mid-October. Snakes appeared to den singly, as we never observed other snakes near our radiotelemetered animals in the winter.

Although snakes moved less in winter than summer, there was some winter movement. The female snake moved at least 11.1 m between 15 December and 13 January. One of the male snakes moved at least 1.2 m every month.

DISCUSSION

POPULATION SIZE AND DENSITY

The lack of information on snake populations is one of the greatest obstacles to snake conservation efforts (Dodd 1993). Usually, only anecdotal information about populations is available. People familiar with Barfoot have reported that the density of *C. pricei* at the site has declined noticeably over the last decade (B. Starrett, pers. comm.). However, there is no baseline data that could be used to support or refute these statements. In fact, abundance and density estimates have never been obtained for *C. pricei* anywhere.

Reasonable estimates of snake numbers are difficult to obtain, largely because snakes are secretive animals. Long-term studies are needed to capture enough snakes to successfully model the population. This requires the use of open population models (because immigration, emigration, births, deaths, and collecting will occur over the study period) that require larger sample sizes for useful estimates than some of the available closed population models.

Population estimates obtained for Barfoot (96) and Site 1 (54) are probably reasonable, due to the relatively large sample sizes (72 and 35 capture events at each site, respectively). Estimates for Site 2 and Site 3 are probably far less realistic due to the small sample sizes (13 and 6 capture events, respectively).

The density index we generated indicates that snakes reach the highest densities at Barfoot and lowest densities at Site 2. We cannot use this information to determine the “health” of the populations at any site due to the lack of baseline data with which to compare it. However, we now have a baseline which can be used to monitor these populations in the future (see “Long-Term Monitoring” section).

SIZE DIFFERENCES BETWEEN AREAS

On average, the Barfoot snakes were smaller than the snakes at the unhunted sites. There are several possible explanations for this. Although the adult: juvenile ratio between sites did not differ greatly, it is possible that the reproduction rate is higher at Barfoot than the other sites. The SVL histograms reveal a proportionally large number of snakes between 200 and 250 mm at Barfoot that may reflect the site's suitability for successful reproduction.

Aspect may play a role in size differences between sites, as snakes tended to be smaller on south-facing slopes than on west-facing slopes. The additional sunlight available on south-facing slopes may be important for females attempting to reach high body temperatures to achieve maximum embryo development. Barfoot was also the lowest elevation site, so the resulting warmer temperatures may aid embryo development there.

Most of the unhunted snakes were captured at Site 1 (61%). The Rattlesnake Fire of 1994 may have affected the population structure at this site. Although it seems unlikely that snakes in the talus would have high mortality as a result of the fire, it is possible that food chain effects might have limited reproduction for a few years. The intense fire around the slope killed virtually all plant life in the area and burned down to mineral soil. This surely resulted in a substantial loss of decaying organic matter at the site and could have precipitated a decline in arthropod populations, which would negatively affect the *Sceloporus jarrovii* population, the main prey item of *C. pricei*. Low food intake has been shown to reduce mean clutch size in viviparous snakes (Seigel and Ford 1992).

Therefore, a lack of food resources at Site 1 may have limited the ability of female *C. pricei* to obtain enough energy to produce the usual number of offspring, which in turn raised the average SVL of the population. A proportionally small number of snakes between 300 and 350 mm SVL (compared to Barfoot) suggests a paucity of young adult snakes in the Site 1 population, which might coincide with snakes born in the years immediately subsequent to the fire. If this hypothesis is correct, average snake size should decrease at the site over the next few years as food resources become more abundant and reproductive output increases.

Another potential explanation of smaller average snake size at Barfoot could be snake collecting. We have established that a substantial amount of collecting has occurred at Barfoot over the last 83 years (see "Twin-Spotted Rattlesnake Collecting" section). When snakes are collected from a discrete area, one would expect the average body size of the population to decrease because proportionally fewer snakes will survive long enough to grow large. This concept can be illustrated with a simple binomial probability equation, which reveals that if 10% of the population is removed by collectors every year, an individual *C. pricei* has a 90% chance of surviving to the age of one year, but only a 67% chance of surviving for five years. Therefore, hunted populations should be younger, and hence smaller, than unhunted populations. Also, due to the small size of *C. pricei* rattles, the larger snakes are much easier to detect than the smaller snakes, which should result in the preferential removal of larger snakes from the population by collectors.

A decrease in average size over time has been reported for eastern diamondback rattlesnakes (*Crotalus adamanteus*) in Florida, with average length decreasing from 1.5-1.7 m in 1929 to 1.2-1.4 m in 1961 (Neill 1961). The role of snake hunters in this size difference is unknown, although the cause is probably anthropogenic and rattlesnake hunting was apparently intense in Florida in the mid-20th century.

A stronger case for a hunting-induced size change in a reptile species was made in a study of the effects of hunting on American alligators (*Alligator mississippiensis*) in Louisiana (Joanen et al. 1997). Hunting of the species was severe, with approximately four million animals taken between the birth of a market for alligator leather in the fashion industry in the late 1860's and the protection of the species in 1962, resulting in a noticeable decrease over time in the average size of alligators killed.

In the 1970's and 1980's, law enforcement agents knew of a Tucson resident who paid people to collect mountain spiny lizards (*Sceloporus jarrovii*), which were then resold. This dealer smuggled the lizards into Mexico and then brought them back into the U.S. under a Mexican collecting permit. Although sufficient evidence for conviction was never obtained, authorities estimated that approximately 10,000 *S. jarrovii* were taken from southern Arizona's sky islands, primarily from areas with road access. Biologists visiting these sites noted that the number of large adult lizards seemed to have declined (C. Lowe and C. Schwalbe, unpublished data).

A comparison of hunted and temporarily unhunted populations of capybara (*Hydrochaeris hydrochaeris*) showed an increase in the average mass, as well as a proportional increase in the older age cohorts, of the unhunted population (Herrera 1992). Young adults were proportionally more abundant in this hunted capybara population as well as others (Cordero and Ojasti 1981). Adult capybaras are usually preferentially hunted.

The *C. pricei* SVL histograms (Figure 2) show that, although Barfoot has some large snakes, the number of large adult snakes between 450 and 500 mm is much smaller proportionally than at unhunted sites, with young adults (300-350 mm) relatively more abundant at Barfoot. Therefore, collecting pressure is likely at least a contributing factor to these differences in population structure at Chiricahua sites.

GROWTH

Growth rate seemed to be most related to the size of snakes, with smaller snakes growing at a faster rate than larger snakes. Kauffeld (1943b) reported an average growth rate of 0.73 mm/ day for the first 135 days in the lives of five *C. pricei* neonates fed in captivity. Although these snakes likely grew faster than wild snakes, this is still a much faster growth rate than we estimated for small snakes (0.34 mm/ day), suggesting that neonate growth is particularly rapid. Large snakes (> 430 mm SVL) grew little over the course of the study, and radiotransmitters did not seem to affect growth.

SIZE RELATIONSHIPS OF MONTANE RATTLESNAKES

A recent AGFD report indicated that Arizona's other two protected montane rattlesnakes, *C. w. willardi* and *C. lepidus klauberi*, exhibit sexual size dimorphism with males being larger on average than females (McCrystal et al. 1996). Klauber (1972) measured 97 adult *C. l. klauberi* and found that males exceeded females in mean total length by 17.2%. In *C. pricei*, we found that the average SVL of each sex did not differ greatly, although the largest three snakes were males, as were eight of the ten largest snakes. On average, adult males were only 3.6% larger than females in total length.

McCrystal et al.(1996) reported length-mass relationships for *C. lepidus klauberi* (n = 39) and *C. w. willardi* (n = 29) from the Patagonia and Huachuca Mountains, indicating *C. pricei* to be the thinnest of the montane rattlesnakes at small body lengths. At 200 mm SVL, *C. willardi* is about 20% heavier than *C. lepidus*, and *C. lepidus* is about 25% heavier than *C. pricei*. However, *C. pricei* has the highest gain in mass for a given gain in length. A 400 mm *C. pricei* is about 8.2 times heavier than a 200 mm *C. pricei*, but the ratio of these masses is only about 7.2 for the other species. As a result, a 465 mm *C. pricei* has the same mass as a *C. lepidus* of the same length.

SURVIVAL ESTIMATES

Although the point estimates for snake survival rate over the course of the study (90-96%) seem reasonable, at least for adults, the confidence intervals for the estimates are wide, precluding comparisons of survival rate estimates among sites. The number of recaptures was too low to accurately estimate survival. We are unaware of any published survival estimates for small, montane rattlesnakes. Potential sources of mortality at our study sites include collectors, other predators (e.g. raptors, black bears (*Ursus americanus*), coatis (*Nasua narica*), ringtails (*Bassariscus astutus*), and skunks (*Mephitis* spp.)), freezing, and rockfall. *C. pricei* can live for over 15 years, 8 months in captivity (Snider and Bowler 1992). Long-term population monitoring will be necessary if reliable survival estimates are desired for sites in the Chiricahuas.

DIET

Our information on diet and other behavioral observations suggest that *C. pricei* feed most when the monsoons first arrive in July. In August and early September mating becomes a priority so snakes spend less time hunting for food. Food boli were found in only one out of 17 gravid females, which is consistent with the fasting behavior reported for other gravid rattlesnakes (Rubio 1998). In late September, after the mating and parturition period, snakes once again resume hunting to build up fat stores for the long winter. We did not find any evidence of a seasonal or ontogenetic shift in prey preference.

Lizards were identified as the primary food item of twin-spotted rattlesnakes long ago (do Amaral 1927). Subsequent field observations in southeastern Arizona consistently reported *Sceloporus jarrovii* as the most frequent prey (Gloyd 1937, Kauffeld 1943a, Woodin 1953). Klauber (1972) also reports that *C. pricei* diet is composed primarily of lizards, having found lizard remains (including *S. jarrovii*) in nine specimens. The only other lizard species reported taken by *C. pricei* in the literature is a single crevice spiny lizard (*Sceloporus poinsettii*) (Armstrong and Murphy 1979).

Prey other than lizards are rarely mentioned. An adult *C. pricei* reportedly disgorged a “field mouse” in the Pinaleños (Klauber 1972). Field guides include small mammals as well as lizards in their overviews of twin-spotted rattlesnake diet (Behler and King 1979, Stebbins 1985, Lowe et al. 1986). Martin (1974) hypothesized that the snakes eat lizards, small rodents, and invertebrates, but does not explain how he arrived at this conclusion. The role of invertebrates in the diet of *C. pricei* is debatable, as it is difficult to determine whether arthropod exoskeletons found in feces represent insects eaten by the snakes themselves or by their insectivorous lizard prey. *C. pricei* have been observed preying on yellow-eyed junco nestlings (*Junco phaeonotus*) near Rustler Park in the Chiricahuas on three occasions (Gumbart and Sullivan 1990). Yellow-eyed juncos are ground-nesting birds common at high elevations in the range.

Our findings add further support to the idea that lizards, in particular *S. jarrovii*, are the most important prey item for *C. pricei*, at least in the Chiricahua Mountains. Radiotelemetry data suggests that *C. pricei* is usually more active during the day than at night, even in the summer. Therefore, a heavier reliance on diurnal lizards than nocturnal mammals for food is not surprising.

Klauber (1972) hypothesized that twin-spotted rattlesnakes are forced to live in areas with abundant lizard populations because the neonate snakes are too small to eat rodents. However, mammal hairs found in a very small snake (SVL = 240 mm, mass = 7.6 g) indicate that even young *C. pricei* can take mammal prey when the opportunity arises. In fact, small mammals seem to be a more important food source than previously recognized, perhaps especially for snakes that are not on talus. The canyon wren in one of our samples, combined with the yellow-eyed junco observations of Gumbart and Sullivan (1990), provide further evidence that *C. pricei* diet is more diversified than we might have expected.

Cannibalism is a widespread phenomenon, occurring in almost all major vertebrate and invertebrate groups (Elgar & Crespi 1992). Studies have indicated that cannibalism is a constant but small part of the diet of many reptiles (Polis and Myers 1985). Prior to this study, cannibalism had been documented in 191 reptile species (Mitchell 1986).

Conspecific ingestion has been documented in several rattlesnake taxa in captivity, including the western diamondback rattlesnake (*C. atrox*) (Klauber 1972), banded rock rattlesnake (*C. lepidus klauberi*) (Williamson 1971, Harris and Simmons 1977), hybrid speckled rattlesnake (*C. mitchellii stephensi* x *pyrrhus*) (Porter 1983), southern Pacific rattlesnake (*C. viridis helleri*) (Powers 1972, Lillywhite 1982), northern Pacific rattlesnake (*C. viridis oreganus*) (Hathcock 1937), and prairie rattlesnake (*C. v. viridis*) (Cunningham 1959, Bullock 1971, Klauber 1972). This sometimes involves two snakes starting to swallow the same prey item from different ends, with neither snake ever retreating (Klauber 1972).

Few instances of cannibalism are reported from wild rattlesnakes. There are three reports of *C. v. viridis* inside wild-caught *C. v. viridis* (Gloyd 1933, Klauber 1972, Genter 1984), and one record of a wild eastern massasauga (*Sistrurus c. catenatus*) eating a conspecific (Ruthven 1911). In at least two of these cases, there is reason to believe that the depredated snake had already died of other causes when eaten. A third species, the Colorado Desert sidewinder (*C. cerastes laterorepens*), was found in the stomach of a conspecific collected from Yuma County, AZ (Funk 1965).

In most instances of cannibalism in reptiles, the prey is a young animal, suggesting that the predator is simply feeding opportunistically on anything it can subdue (Polis and Myers 1985). Others have suggested that cannibalism in snakes may occur when chemosensory-based recognition systems fail (Mitchell 1986). Given the large size difference between predator and prey in our observation, the former hypothesis is plausible, while the latter cannot be evaluated.

REPRODUCTION

We are the first to document copulation in wild *C. pricei*; further, combat has never been observed outside of captivity, as most information about reproduction comes from animals in zoos and other collections.

Combat between two male *C. pricei* was observed on 10 July 1984 at the Arizona-Sonora Desert Museum, with subsequent copulation after the less successful male was removed from the cage (Mahaney 1997b). A litter of five was born to the female the following year on 6 June. Only one other successful captive mating is reported in the literature, with four (three live) young born on 9 July (Armstrong and Murphy 1979).

More typically, births are reported for captive *C. pricei* that became impregnated while they were still in the wild. Snakes collected from Barfoot have given birth on 18 August and 4 August (Kauffeld 1943b, Mahaney 1997a). Another *C. pricei* from the Chiricahuas gave birth on 20 May (Armstrong and Murphy 1979). A *C. pricei* presumably collected from the Pinaleños produced young on 3 August (Kauffeld 1943b). Snakes from Durango, Mexico gave birth on 10, 14, 27, 29, and 24-28 July (Armstrong and Murphy 1979). A snake collected in Chihuahua, Mexico gave birth on 19 July (Van Devender and Lowe 1977). Five fully-formed embryos were found in each of two snakes collected on 27 August from Chihuahua (Tanner 1985). Finally, a *C. pricei* of unspecified origin gave birth on September 23 (Keasey 1969). These dates suggest that July and August are the primary parturition months for *C. pricei*, but information obtained from captive animals may not accurately reflect their behavior in the wild.

Determining the precise number of embryos in a *C. pricei* by palpation is difficult, as embryos are often bunched closely together and must be handled gently. Therefore, our estimate of 3.85

embryos per clutch is likely biased low. Based on 14 records in the literature and the parturition event from our study, the average litter size for *C. pricei* is 5.80 (SE = 0.45, range = 3 to 9).

Observations and data from this study suggest that most mating occurs during August and early September in the Chiricahuas. Females apparently store sperm over the winter. Our radiotelemetry data, although limited, suggests that gravid females are fairly mobile until around mid-July, after which they remain in a small area. On average, embryos and associated tissues comprise about 39% of the mass of gravid snakes, so limited mobility is probably one reason these snakes confine themselves to a small area during pregnancy. All three of the radiotelemetered snakes that gave birth moved large distances in late August or early September, most likely immediately or soon after parturition. Large movements by females following the cessation of maternal duties has been observed in blacktail rattlesnakes (*Crotalus molossus*) (D. Hardy, pers. comm.). Two of our gravid radiotelemetered snakes were observed in close proximity to adult males after these large movements, but it is unknown whether the males successfully copulated with those females.

HABITAT

Although 66.3% of the observations of snakes on talus were within 5 m of the edge, they are not necessarily more concentrated there because we focused about 70% of our search time in those areas. However, 93.0% of the observations were within 5 m of vegetation, suggesting that they do have an affinity for vegetative cover. At Barfoot, they did not seem to be selecting any particular type of plant out of proportion to its abundance. We did not notice any differences in habitat use between talus slopes that seemed biologically important. Our radiotelemetry data suggest that *C. pricei* also spend time off talus, and are not even always associated with rocky areas.

MOVEMENTS

Although there have been few comparative studies of snake movements, some indicate that gravid females tend to move less than non-gravid females, and that non-gravid females move about as far as males (Macartney et al. 1988). Our data are consistent with these findings. Gravid *C. pricei* females seem to remain more or less stationary between mid-July and the end of pregnancy in late August or early September, and subsequently make significant movements to find prey. The timing of these events may vary from year to year, and probably by location. We only tracked one non-gravid female (in 1997), but she moved farther during the monsoon months than both the 1998 gravid females and the 1997 males.

One of the more dramatic findings from the radiotelemetry study is the large difference we observed in male activity between years - males moved over six times farther per week in 1998 than 1997. Mate searching is thought to be the primary explanation for large movements by male rattlesnakes during the breeding season (Rubio 1998). One possibility, then, is that male snakes were more interested in mating in 1998 than they were in 1997. However, we detected no obvious difference in sexual activity between years.

Reptile activity is often dictated by weather conditions, and weather may be the underlying cause of yearly differences we observed in snake movement. The 1997 monsoon season was longer (1997: ~ 66 days, 1998: ~ 48 days) and approximately 30% more rain fell in 1997 than in 1998 at nearby Chiricahua National Monument. Also, in 1997, 60% of the rain during those months fell in August, whereas in 1998, over 75% fell in July.

Thus, August and September were much drier in 1998 than in 1997. The reduction of intense rains in those months in 1998 likely correlated with a corresponding decrease in cloud cover. The sunnier, drier weather in 1998 may have increased the talus surface temperature to a point where snake activity on the talus was limited. Perhaps males and at least non-gravid females moved off talus into the cooler, more favorable microclimates found in the vegetated areas surrounding the talus. The talus, with its relatively high prey density and extensive cover, may act as a concentrator of *C. pricei*. When *C. pricei* are forced off talus, they become more dispersed, so males may have to move farther and more often to locate females. Although this hypothesis is fairly speculative, it would explain both the increased male movement and the shift from talus to non-talus areas between 1997 and 1998.

In 1998, we found that the males at Barfoot moved shorter distances on average than the non-Barfoot males. Although we can only speculate on the potential reasons for this difference because of the very small sample size, it may be related to the apparent higher density of snakes at Barfoot. In an area of higher population density, it seems likely that male snakes would not have to travel as far to find mates. A higher prey density at Barfoot could also be a factor. It seems unlikely that this difference in movement pattern between sites could be related to collecting.

WINTER ACTIVITY

C. pricei select warm microclimates during the colder months that permit some activity throughout the year, even at high elevations. We do not know if *C. pricei* eat in the winter, but their primary prey item, *Sceloporus jarrovii*, is active in at least one of the study areas during this season. On 24 November 1997, 97 *S. jarrovii* were observed basking on two cliff faces above the Barfoot talus at about 2,560 m (8,400 feet). Basking *S. jarrovii* were observed at the same location on 15 December 1997 and 19 March 1998. Bunch grass lizards (*Sceloporus scalaris*) were observed on 16 December 1997 at Site 2 and on 7 December 1998 near Barfoot, surrounded by snow. These winter observations provide further insight into the unique nature of the cold-adapted herpetofaunal communities of Arizona's sky islands (Ruby 1977, Congdon et al. 1979).

TWIN-SPOTTED RATTLESNAKE COLLECTING

METHODS

HISTORICAL

To assess historical pressure by snake collectors, we reviewed published accounts of collecting activities in the Chiricahuas, interviewed people closely associated with the reptile trade, and reviewed records from twelve U.S. institutions that have *C. pricei* specimens from Arizona to determine where and when they were collected. The twelve institutions were: Chicago Academy of Sciences, Harvard University, Illinois Natural History Survey, Michigan State University, Natural History Museum of Los Angeles County, Texas A & M, Texas Tech, U.S. National Museum, University of Arizona, University of California - Berkeley, University of Colorado, and University of Texas - El Paso.

REMOTE SENSING

To assess current pressure from snake collectors, we used remote sensing, conducted surveillance, and evaluated habitat destruction associated with snake collecting. Remote sensing methods included the use of seismic sensors. Four sensors were buried along the edge of the largest talus slope at Barfoot in early July 1998. Sensor heads were placed along established talus "trails" which have been created by people searching for *C. pricei* over the years. A transmitter unit with an antenna was connected to each sensor unit, sending a signal to a handheld radio when the talus near the sensor head was disturbed.

Unfortunately, even after numerous attempts to improve the transmission strength and sensitivity of the seismic sensors, we were unable to pick up signals when we were out of sight of the talus, greatly diminishing the utility of this method. We also found that most of the sensors did not reliably send out signals when the sensor head area was disturbed. Possibly, these sensor units are only designed to work in areas with a more compact substrate (E. Herrick, pers. comm.). In addition, despite our best efforts to conceal the units, sensors were discovered by people looking for snakes on at least two occasions.

In another effort to quantify collecting effort through remote sensing, we concealed a camera (Trailmaster, Lenexa, KS) among the cliffs above the largest talus slope at Barfoot on 1 September 1998. An intervalometer (Trailmaster, Lenexa, KS) was used to signal the camera to take one picture per hour between 0800 and 1800 throughout September.

The Trailmaster camera proved to be less useful than anticipated. Due to technical difficulties with the equipment, the small number of photos taken (n = 40), the limited field of vision, and, perhaps, the large distance between the camera and the talus slope, no people (including the authors) were detected on the talus through the use of this method.

SURVEILLANCE

Direct covert surveillance of the study sites usually involved concealing ourselves in a location where any individuals on the talus would be visible through binoculars. Occasionally, surveillance was instead conducted by camping at Barfoot and posing as a birdwatcher.

On 15 and 16 August 1997 (Friday and Saturday), we observed the Barfoot slopes through binoculars hourly between 1100 and 1800. During Labor Day weekend, a more concerted effort was made to surveil all of the slopes. On 29 August 1997 (Friday), Barfoot was observed continuously from 1100 to 1900 and Site 2 was observed from 1545 to 1800. On 30 August, Barfoot was observed continuously from 0800 to 1900, Site 1 was observed from 1700 to 1815, and Site 2 was observed from 0730 to 1415 and 1645 to 1715. On 31 August, Barfoot was observed from 0800 to 1515, Site 1 was watched from 0700 to 1115, Site 2 was observed from 0800 to 1200, and Site 3 was watched from 1330 to 1515. Finally, on 1 September, Barfoot was watched from 0745 to 1815.

Due to a lack of success in 1997, we only conducted two days of surveillance in 1998, both at Barfoot. The talus was observed on 1 August (Saturday) from 0700 to 1700 and on 2 August from 0630 to 1320.

INCIDENTAL OBSERVATIONS

Most collectors were observed incidentally while we were conducting other activities. All individuals observed on the talus who were clearly looking for snakes were identified as collectors. Some people on the talus were excluded from the "collector" category because we deemed it unlikely that they were looking for snakes. We did not differentiate between people who claimed to just be interested in photographing the snakes and other people who were more obviously interested in collecting because collectors often pose as photographers (C. Scott, pers. comm.).

We tried to avoid direct contact with collectors, but were occasionally approached. When questioned, we posed as birdwatchers if we were off talus or as mountain spiny lizard (*Sceloporus jarrovii*) researchers if we were observed on talus. We used this deception due to concerns that if it became common knowledge among collectors that we were studying *C. pricei*, they might temporarily stop collecting at our study sites for fear of being reported. This would obviously bias our estimates of numbers of collectors. Usually we could not watch collectors closely enough to determine how many snakes (if any) each group captured.

The number of collectors observed each year between July and September (the peak activity period for *C. pricei* and their collectors) was tallied. Collectors recorded during formal surveillance periods and through incidental observation were pooled. The number of hours spent at each site during daylight hours (defined as 0800 to 1900) when we would have probably detected collectors was also compiled. The number of collectors was divided by the number of observation hours to generate a "collectors per hour" figure. This figure was multiplied by the total number of daylight hours between July and September (1,012 hours) to estimate the total number of collectors during those months for each year.

HABITAT DESTRUCTION

Habitat destruction was documented by taking 6 to 77 photographs (based on the amount of talus) of each site each year. Evidence of habitat destruction included "trails" across the talus, large pits in the talus, and overturned rocks. Overturned rocks could be identified at most sites by a lack of lichen on the uppermost rock surface.

RESULTS

HISTORICAL

Twin-spotted rattlesnake collecting by European-Americans began in the summer of 1893 when W.W. Price, the avid mammal, bird, and reptile collector for whom the species is named, led an extensive expedition through southeastern Arizona. Five of the 700+ reptile specimens Price brought back to Leland Stanford Junior University belonged to a new species of rattlesnake, *Crotalus pricei* (Van Denburgh 1895). Most, if not all, of these *C. pricei* specimens were collected in the Huachuca Mountains (Van Denburgh 1896).

Before long the Chiricahua Mountains came to overshadow the Huachucas as a locality for *C. pricei*. H.K. Gloyd, accompanied by a student named Hobart Smith, captured *C. pricei* in the Chiricahuas in the early 1930's (Gloyd 1937). L.H. Cook collected 30 twin-spotted rattlesnakes in the Chiricahua Mountains in 1931 for the San Diego Society of Natural History (Klauber 1972). Cook was perhaps among the first to mention Barfoot Park as a *C. pricei* site; he cited other localities in the Chiricahuas as well. By 1936, enough twin-spotted rattlesnakes had been collected for Klauber (1936) to have access to 107 specimens, probably from various mountain ranges.

A herpetologist named Carl Kauffeld took a great interest in *C. pricei* as well as Arizona's other montane rattlesnakes. Wright and Wright (1957) write:

> "No one has spent more time and effort on the smallest species of rattlesnakes (Price's, Willard's, and green rock rattlesnakes) than Kauffeld, and anyone who goes to their haunts hears the echoes of his footsteps and searches in Arizona's southern mountains. And young bloods compare their successes or failures with his results."

In addition to contributing much to the small pool of previously existing knowledge about the species, Kauffeld was probably the most influential publicist for Barfoot as a collecting site. He captured three *C. pricei* at Barfoot for the Staten Island Zoo in 1941, but had a more profound impact on the Barfoot population by mentioning the site by name and publishing a photograph (Kauffeld 1943a). Kauffeld also featured Barfoot in subsequent publications, including two well-known books about snake collecting, "Snakes and Snake Hunting" (1957) and "Snakes: the Keeper and the Kept" (1969). These books were recently reprinted and are still used frequently by snake collectors.

Kim Murphy, wildlife manager for the Chiricahua Mountains from 1965 to 1998, noted a sharp increase in collecting at Barfoot following the publication of the latter book (K. Murphy, pers. comm.). This rise in collecting occurred despite Kauffeld's plea to reduce the amount of collecting at the site:

> "[Barfoot] has been hit too hard and too often in recent years by collectors. True, the species is one that is plentiful in the Chiricahuas, but Barfoot is too convenient, and few if any of these collectors care to take the time and trouble to search for other concentrations- nor do they show any restraint in the numbers they take." (Kauffeld 1969)

Kauffeld also believed that the twin-spotted rattlesnake population at the site had already been noticeably impacted by collectors. After finding fewer *C. pricei* than he had anticipated during an afternoon at Barfoot with Robert Stebbins and Bill Woodin, Kauffeld wrote:

> "...three in nearly two hours of search under favorable conditions is hardly indicative of numbers. Could it be that even then, almost ten years ago, the population was suffering from overcollecting?" (Kauffeld 1969)

Kauffeld was not the last to publicize Barfoot. Herp collectors searching for twin-spotted rattlesnakes can read about Barfoot and view a photograph of the site in a newer guide book, "The Venomous Reptiles of Arizona" (Lowe et al. 1986). Some other recent herp collecting books do not mention Barfoot by name (e.g. Williamson 1986), perhaps reflecting a growing sensitivity about revealing precise locality information.

REVIEW OF SPECIMENS

The twelve institutions selected owned a total of 93 *C. pricei* specimens from Arizona. By 1936, at least 107 specimens had already been collected by institutions, so our data constitutes a small fraction of available specimens (Klauber 1936). Two of the specimens had no locality information or a locality that was obviously incorrect. Of the 91 remaining specimens, at least 41% were collected at Barfoot. The percentage may actually be higher, but four Chiricahua records did not include site-specific locality or elevation information.

The Chiricahua Mountains accounted for most of the specimen origins, with 74% having been collected in the range. Eleven percent of the specimens were collected in the Huachuca Mountains, 9% in the Santa Rita Mountains, and 6% in the Pinaleños. The earliest record from the Chiricahua Mountains is from 1904. The first mention of Barfoot appears with two specimens collected in 1916.

The Arizona Natural Heritage Program Database, which includes both specimens and sight records, gives similar statistics regarding *C. pricei* records (Johnson and Mills 1982). Of 178 records, 42% are from Barfoot and 78% are from the Chiricahuas.

Most of the dated specimens from the twelve institutions were collected in the 1950's (53%). The 1960's was the next most prolific decade of collection (21%). Nineteen percent of the specimens were obtained between 1900 and 1949. Over the last thirty years, only two snakes have been collected per decade, and both snakes from the 1990's were found dead on roads.

Given that Klauber had access to 107 *C. pricei* specimens in 1936, the fact that most specimens in the collections we studied dated from the 1950's and 1960's, and our finding that over 40% of the specimens were collected at Barfoot, the total number of *C. pricei* collected at Barfoot for scientific purposes during the 20th century must number in the hundreds.

If we assume that our specimen dates and localities accurately reflect the collecting trend over the century and that 107 *C. pricei* were collected from sites in Arizona between 1900 and 1939, we arrive at the estimate that 695 *C. pricei* were collected in Arizona during this century for scientific institutions, including at least 285 from Barfoot. More than half of these snakes presumably would have been collected in the 1950's (Figure 7).

INTERVIEWS

Kim Murphy observed numerous twin-spotted rattlesnake collectors at Barfoot between the mid-1970's and mid-1980's. He attributes some of the collecting during that period to researchers and zoo employees with scientific collecting permits. Nonetheless, he also noted an increase in illegal collecting during that period. According to Murphy, the snakes were worth about $150 each at that time and the chances of being caught were

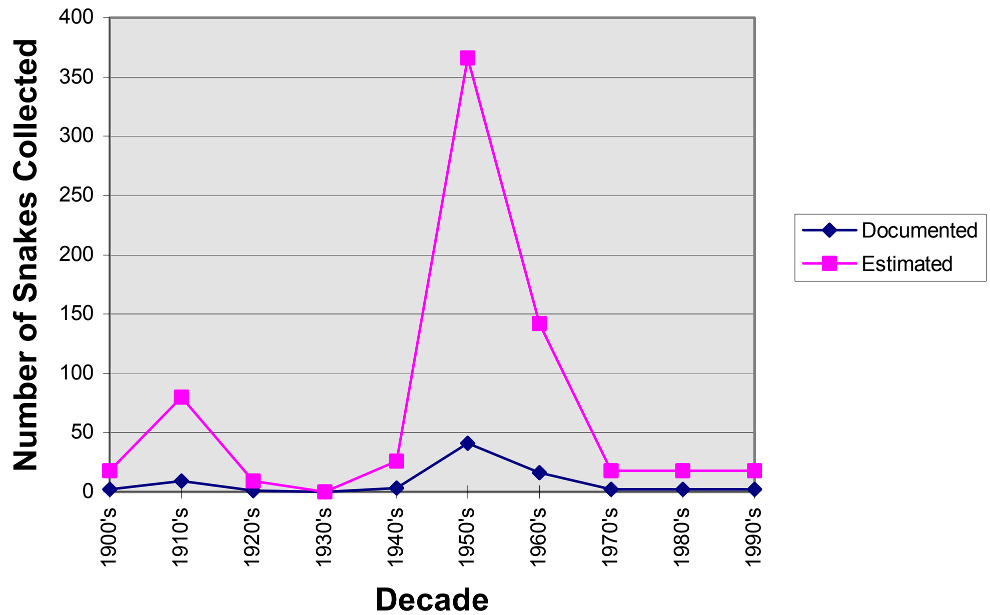

Figure 7. General trends in twin-spotted rattlesnake specimen collecting over the 20th century

extremely slim, making collecting of the species particularly attractive. He attributes an apparent decline of Barfoot collectors over the last decade to increased efforts on the part of law enforcement agencies and a possible saturation of the market.

Chris Scott, formerly with the National Park Service's Resource Protection Unit, reports that large numbers of twin-spotted rattlesnakes are still being collected from Barfoot for the pet trade, and that the trade in reptiles is increasing.

CURRENT COLLECTING

Although our covert surveillance of Barfoot and the other study sites resulted in the detection of only two collectors, we incidentally observed numerous people searching for twin-spotted rattlesnakes. During the 726 daylight hours we spent at Barfoot in 1997 and 1998, we observed 37 people in 14 groups on the talus. We spent 294 daylight hours at Site 1, 200 hours at Site 2, and 57 hours at Site 3, but did not observe any people on talus at those sites.

In 1997, we observed 17 individuals on the Barfoot talus, 8 in July (in three groups) and 9 in August (in five groups). The first collectors were observed on 25 July and the last were seen on 14 August. Two of the individuals were counted twice because they were observed on two different, non-consecutive days. Three other people were observed in August on the Crest Trail walking south from Barfoot, two of whom were wearing gloves that looked like welding gloves (commonly used to capture small rattlesnakes). These three individuals were not counted as collectors because we did not observe them on the talus.

In 1998, we observed 7 people on the Barfoot talus who seemed to be looking for snakes, 6 in August and 1 in September. The six August individuals were in three groups. In mid-September, somebody pulled a seismic sensor head out of the talus. This happened before the September collector was observed, but the individual(s) who located our hidden equipment were not counted because they were not actually observed. The seven people identified as collectors were observed between 1 August and 28 September.

In 1997, we spent 255 daylight hours at Barfoot during the prime collecting season, July to September, resulting in an observation rate of 0.067 collectors per hour or 15.0 observation hours per collector. In 1998, we spent 329 hours at Barfoot, resulting in 0.021 collectors per hour or 47.0 observation hours per collector. Extrapolating to cover every day from July through September, we estimate that there were 67.6 and 21.6 collectors for each year, respectively, or a total of 89.2 collectors at Barfoot for both years during those months (Figure 8).

HABITAT DESTRUCTION

We noted a well-worn system of trails at Barfoot that skirt along the edges of the talus and connect to the vegetation islands on the slope (Figures 9 and 10). Although we

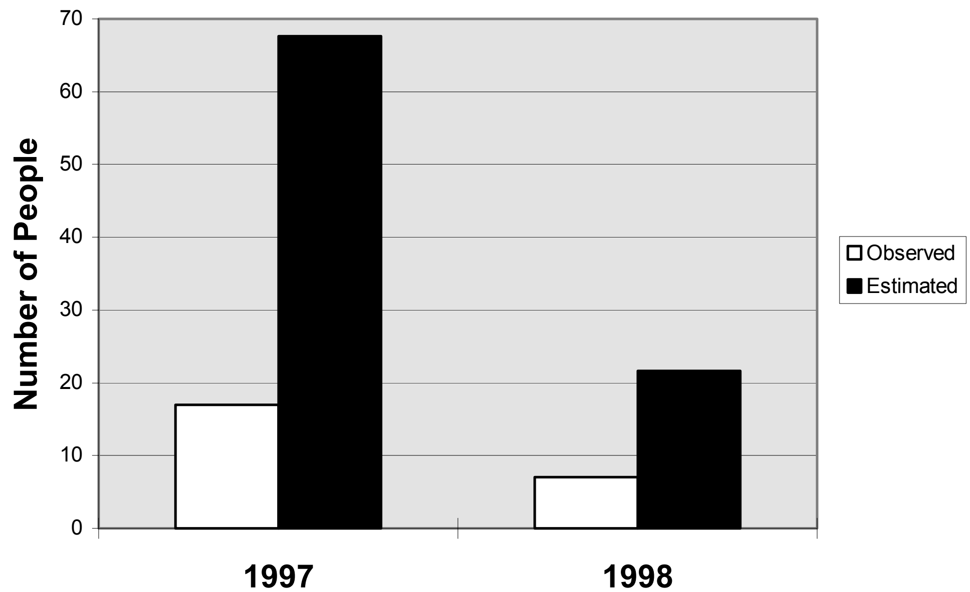

Figure 8. Twin-spotted rattlesnake collectors at Barfoot

Figure 9. Talus trail leading to vegetation island at Barfoot

Figure 10. Trail around edge of talus at Barfoot

contributed to the erosion of those trails during our study, they were already well-established before we began. No trails were visible at Sites 1, 2, or 3 at the beginning of the study. By the end of the study, faint trails were apparent in some areas at those sites. This habitat disturbance was surely primarily, if not solely, due to our activities.

A comparison of the Barfoot photographs with photographs from the other sites show a greater proportion of overturned rocks at Barfoot. This difference is probably primarily due to collectors not associated with this study.

We observed large pits in the talus near the base of the slopes at Barfoot, including the slopes in our study area as well as the large west-facing talus slope below the Barfoot lookout tower (Figure 11). No such pits were observed at the other study sites. These pits may have been excavated by collectors pursuing fleeing twin-spotted rattlesnakes.

DISCUSSION

HISTORICAL

Prior to the 1960's, researchers may have constituted the greatest human threat to twin-spotted rattlesnake populations. At the time, a major goal of many field biologists was to collect as many animals as possible and preserve them in alcohol for future study. Van Denburgh (1922) illustrates the prevalent view of biologists during this era: "...the collector should strive to secure many specimens of each species."

Our review of records indicated that more *C. pricei* specimen collecting occurred at Barfoot than any other site. If the trends revealed by our review of museum specimens are accurate, over 140 snakes may have been collected at the site in the 1950's, giving Kauffeld (1969) good reason to wonder if the Barfoot population had noticeably declined when he visited the site around 1960.

Although preserved specimens can yield useful information regarding species distributions, diet, reproduction, morphology, pathology, and other important biological aspects, there has been a strong trend among biologists away from collecting large numbers of specimens over the last thirty years. This trend is clearly indicated by our specimen data, which show a drastic decrease in scientific collecting after the 1960's, and finally the procurement only of roadkilled *C. pricei* in the 1990's. This sharp decline probably also reflects the decision of the Arizona Game and Fish Commission to protect the species in the early 1970's. Collecting still occasionally occurs at Barfoot for zoo exhibits (e.g., Mahaney 1997a). However, today the main threat to *C. pricei* and other protected montane rattlesnake populations is surely the black market pet trade.

Figure 11. Pit on talus slope below Barfoot lookout tower

Collecting of *C. pricei* at a fairly large scale has clearly continued since the state officially ended legal collection of the species. One herpetologist echoed Kauffeld's earlier concerns about twin-spotted rattlesnake collecting:

> "In the Chiricahua Mts., large talus slopes which once provided sanctuary for large numbers of Twin-Spotted Rattlesnakes have become almost "sterile" of this species in recent years." (Martin 1974)

Kim Murphy observed a peak in snake collecting at Barfoot between the mid-1970's and mid-1980's. Johnson and Mills (1982) shed additional light on the amount of collecting pressure at Barfoot during that period:

> "It is a rare day during the rainy season (July-September) when no snake hunters are encountered in the Barfoot-Rustler Park area of the Chiricahuas.".

CURRENT COLLECTING

Over the course of the study we observed 24 people who were almost certainly looking for snakes at Barfoot, and estimate that there may have been as many as 89 between July and September. There was a substantial difference in the number of collectors observed between years. We observed 17 people (and estimated 68) in 1997, and only observed 7 people (and estimated 22) in 1998, despite the fact that we spent substantially more time at Barfoot in 1998 than 1997. We may have just happened to miss the big collecting days in 1998, but more likely our figures reflect an actual difference in collection pressure between the years.

Although the number of collectors may fluctuate from year to year, we believe our study itself may have reduced the number of collectors at the site in 1998. Despite our attempts to maintain secrecy, enough people probably knew of the existence of the project for word to reach the collectors' communication channels by the second year of the study. Collectors may have feared that we were watching the slopes and would report them.

Some, if not most, of the people searching for snakes were probably more interested in photographing the animals than collecting them. However, even photography has an impact because the snakes are usually captured before they are photographed and, in addition to stressing the animal, the snake may not be returned to its exact capture location. Regardless of the motives of these snake searchers, 89 (or even 24) people is a large number of snake searchers at one site given the protected status of the species.
Although we do not know how many snakes were collected, both our observations and our estimates indicate that a considerable amount of snake collecting continues at Barfoot.

Habitat destruction was only observed at Barfoot, indicating that collecting was non-existent or infrequent at our other study sites. Destruction of habitat due to collecting-related activities has been shown to negatively impact other reptile populations in Arizona (Goode et al. 1998). Given the large size of the talus slopes, overturned rocks, pits, and talus trails probably do not have a major impact on the *C. pricei* populations at our study sites. However, our understanding of the microhabitat requirements of *C. pricei*, particularly during the winter, is limited, and disturbance may have an important adverse effect in certain discrete areas of these slopes. Also, *C. pricei* often inhabit areas other than large talus slopes. In those areas of less abundant cover, habitat destruction may be a major concern. Regardless of the direct impact on the snakes, evidence of disturbance provides useful information about the extent of collecting activity in a given area.

CROTALUS PRICEI AND THE PET TRADE

Although collecting pressure at Barfoot may have diminished somewhat since the mid-1980's, illegal collecting is still apparently common at the site. In 1995, a reptile pet dealer in Florida had 20 adult *C. pricei* for sale at $350 each (C. Scott, pers. comm.). Although some snake species are bred in captivity, the majority of the snakes in the pet trade are wild caught (Dodd 1987). Many of these *C. pricei* were probably captured at Barfoot.

This information indicates that twin-spotted rattlesnakes are one of the "priceir" Arizona herps, although they are rarely seen on dealer lists. For comparison, reptile pet dealers are currently selling banded rock rattlesnakes (*Crotalus lepidus klauberi*), another montane species protected in Arizona, for $175, and western diamondback rattlesnakes (*Crotalus atrox*) for $40.

The rarity of *C. pricei* is surely one of the reasons the species is highly valued. However, the legal protection afforded *C. pricei* throughout its range is probably the main reason these snakes are so expensive and so rarely advertised. *Crotalus lepidus klauberi* are similar in size to *C. pricei*, and many collectors believe they are the more attractive of the two species (H. Herrmann, pers. comm.). However, *klauberi* are much easier to purchase and less expensive. Most likely, this is because they can be legally captured in New Mexico. The lack of uniform regulations regarding species protection means that collectors can easily claim that their animals were caught legally in New Mexico even if they were actually caught in Arizona. Twin-spotted rattlesnakes and the third protected Arizona montane rattlesnake, the ridgenosed rattlesnake (*Crotalus willardi*), apparently are not widely advertised because they are usually sold behind the scenes (C. Scott, pers. comm.). *Crotalus willardi*, like *C. pricei*, is protected throughout its range.

The Arizona Game & Fish Department and federal agencies have worked together to stem the flow of *C. pricei* and other native reptiles from the state. They are denting the illegal herp trade in the state, but the trade is far from broken. Arizona herps are commonly found on price lists, even when those herps were probably not obtained legally. A review of widely-distributed price lists reveals the sale of locality-specific Arizona mountain kingsnakes (*Lampropeltis pyromelana pyromelana*) from the Chiricahua Mountains, Madera Canyon (Santa Rita Mountains), and Carr Canyon (Huachuca Mountains) among other Arizona locations, as well as green rat snakes (*Senticolis triaspis*) from the Santa Rita Mountains. Many reptile dealers post "wish lists" on the internet in which they express their desire for collectors to bring them native reptiles from Arizona. As it has been illegal to sell any Arizona wildlife or its offspring for most of this century, much of this trade clearly violates both Arizona state law and the Lacey Act.

However, once the animals are out of state, prosecuting violators is difficult as law enforcement officials must prove that the animals were collected in Arizona. Collectors often insist that their poached reptiles are captive-bred or were collected in a state where collecting is less regulated, such as New Mexico (Tweit 1997). Even when collectors are prosecuted, fines and penalties are generally small compared to the profits that can be made through illegal sales of reptiles (Wittig 1998).

FUTURE OF COLLECTING AT BARFOOT

Markets for fringe products like pet rattlesnakes tend to be unpredictable and can change quickly. In 1980, John Travolta showcased Indian python (*Python molurus*) boots in the film Urban Cowboy. The film appeared to have an immediate and substantial impact on the reptile trade. The sudden demand for Indian python skins posed a serious threat to the persistence of the species (Potten 1991). Likewise, after Paul Hogan became famous in his reticulated python jacket (*Python reticulatus*) in Crocodile Dundee in 1986, demand for that species endangered populations (Potten 1991). These films may have also had indirect effects on U.S. snakes. The prices and volume of rattlesnakes sold at the Sweetwater Rattlesnake Roundup in Texas skyrocketed immediately following the release of Urban Cowboy, presumably reflecting a leap in demand for rattlesnake skins (C. Painter, pers. comm.).

The U.S. is not the only country whose whims are dictated to some degree by media. In the early 1980's, a television commercial in Japan featured a frilled lizard (*Chlamydosaurus kingii*), initiating a huge demand for the lizards among Japanese (Fitzgerald 1989). By 1984, a pair of these lizards was worth over $680,000.

If John Travolta, Bruce Willis, Keanu Reeves, or another major movie star are featured in a successful film in which the actor has a pet rattlesnake, the collecting pressure at Barfoot could greatly increase over the short term at least. Undercover law enforcement operations and increased surveillance of the site can help protect the Barfoot population now and prepare law enforcement agencies for this kind of unforeseen emergency.

MANAGEMENT OF *C. PRICEI* AT BARFOOT

Due to indications that the worldwide trade in pet reptiles is increasing, we anticipate that the collecting pressure at Barfoot will steadily escalate over the next few years at least. The Barfoot population has clearly withstood a substantial amount of collecting for a long period of time. Therefore, current rates of collecting will probably not eliminate the Barfoot population, although the population will surely be affected in other ways. Based on our own exploration of the Chiricahua Mountains, we believe that Barfoot is the most important *C. pricei* locality in the range. Other south-facing talus slopes that compare in size to Barfoot are rare. We believe it is essential to continue efforts to reduce the impact of collecting on the Barfoot population.

One of the main reasons Barfoot has been, and will continue to be, a major collecting site is the ease of access provided by the road that runs right next to the talus slopes. The U.S. Forest Service is currently planning to reduce the amount of recreational use at Barfoot by removing picnic tables and other structures and closing some of the roads leading to campsites around Barfoot Park. This may help to discourage some of the less serious collectors who primarily come to Barfoot to camp. However, to our knowledge, the road leading through Barfoot Park will remain open, so this action will not discourage most collectors. Also, if fewer people are camping at Barfoot, collectors may be less concerned about being reported and may increase their activity. Nonetheless, we generally support efforts to reduce visitation to the area. We believe that the worst thing that could happen to the Barfoot population would be the paving of Pinery Canyon Road (Forest Road 42), which is the only road giving access to Barfoot and other high elevation areas in the Chiricahuas.

The most important actions AGFD and USFS can take to protect the Barfoot *C. pricei* population are to keep visitation at a relatively low level and to continue to conduct anti-poaching operations. However, AGFD also has direct control over the number of snakes that can be collected legally through the issuance of scientific collecting permits. As far as we can determine, most *C. pricei* collected under these permits are destined for zoos. There is currently no need to institute a captive breeding program for *C. pricei*, so these animals are being collected to attract visitors to the zoo and for their educational value.

Several zoological institutions have recently expressed an interest in mounting collecting trips to obtain *C. pricei* (Mahaney 1997b), and we have been informed that some of these expeditions have recently taken place (S. Mazur, pers. comm., R. Murray, pers. comm.). Although the number of snakes removed by zoo collectors is probably small compared to the number removed illegally, the additive effects of both groups may have an impact on populations. The presence of legal collectors at Barfoot and other Chiricahua sites can also complicate anti-poaching efforts, as local law enforcement officers are usually not given notice (K. Murphy, pers. comm.).

State and federal governments periodically obtain *C. pricei* that cannot be repatriated as a result of undercover law enforcement operations. We recommend that zoological institutions be placed on a wait list for these confiscated animals for a period of time before being issued a collecting permit. If the capture of additional snakes for zoos is necessary, we suggest directing these legal collectors to Barfoot. Although Barfoot is the most heavily impacted *C. pricei* locality in Arizona, the site also supports a relatively large concentration of snakes, and can probably better withstand the loss of a few snakes than smaller populations. Local law enforcement personnel, particularly the wildlife manager, should be kept informed regarding vehicle descriptions of legal collectors and approximate dates of planned collecting activity so time is not wasted in conducting surveillance of collectors with permits.

LONG-TERM MONITORING

The best way to monitor the twin-spotted rattlesnake populations in the Chiricahuas would be to continue this study indefinitely. Unfortunately, funding constraints make this an unlikely scenario. A more realistic approach to monitoring would be to implement a relatively simple, inexpensive, time-efficient process that would enable interested parties to gather enough information to detect drastic changes in the populations. The Barfoot population is of particular concern, as it is clearly more heavily impacted by humans than the others.

We recommend continuing the Barfoot “roundups” that were started in 1997. These are four-day events that rely upon a large number of volunteers to catch as many snakes as possible in a short period of time. Although unlikely that enough snakes will be captured during these events to allow a reasonable estimation of population size or density in a given year, major shifts should be detectable in several ways.

First, an index of density can be calculated each year as long as volunteers keep careful track of the amount of time they spend looking for snakes and record observations as well as captures. If the roundup is held at the same time every year, this index should be roughly comparable across years and should alert organizers if density has changed dramatically. Second, over a period of several years, it should be possible to estimate survival rates more accurately than we can currently. A change in survival rates will signal organizers to investigate further. Finally, the age structure of the population can be modeled based on snout-vent length. A decrease in the proportion of large snakes over time will probably indicate that something (or someone) is shortening the average life span of snakes at the site. An increase in illegal collecting should be suspected.

In addition to monitoring trends in the population, an annual survey will yield information about twin-spotted rattlesnake diet, reproduction, growth rate, and habitat use, all of which are important if the species is to be managed effectively. We recommend holding surveys in late July in order to maximize the number of snakes captured while minimizing the impact on gravid and mating snakes.

Although there are other talus slopes in the area that support twin-spotted rattlesnakes, we believe the Barfoot slopes are most affected by collectors. Undercover law enforcement operations will alert wildlife and land management agencies if collectors begin impacting other sites. Law enforcement staff can also form an essential part of the monitoring system by keeping wildlife managers informed of trends in the reptile trade.

THE BIG PICTURE

Twin-spotted rattlesnakes are unique for many reasons. They are Arizona's smallest and highest elevation rattlesnake, reaching elevations of over 3,050 m (10,000 feet), and seem to thrive in the cold climates associated with those heights. Unlike most rattlesnakes, lizards rather than mammals are the staple diet. In the U.S., these snakes are found in only four or five mountain ranges, all in southeastern Arizona. They are rarely encountered by humans, yet this very rarity makes them marketable to unscrupulous pet collectors striving themselves to achieve a measure of uniqueness in an increasingly homogenized world.

Twin-spotted rattlesnakes have been collected at Barfoot since early in the 20th century. Once sought after in the name of science, they are now hunted for profit. Despite the protection afforded the species by the state of Arizona, snakes are still frequently taken from the site. In fact, the majority of twin-spotted rattlesnakes sold in the lucrative illegal pet trade probably originate at Barfoot, where the snakes are easily accessible and present in relatively high densities.

In our two-year study, we could not determine whether the snake population size has decreased at the site as a result of overexploitation. Only long-term monitoring can reveal long-term trends. However, we detected a difference in snake size between Barfoot and nearby unhunted sites that could be explained by collecting pressure. Our study also uncovered a substantial amount of new information about the ecology of this species that should help future researchers focus their studies and aid wildlife managers in their plans to ensure the persistence of populations.

Barfoot is renowned as a twin-spotted rattlesnake locality for good reason. It supports large prey populations, a variety of microclimates, and provides abundant cover for the snakes. There is no other locality, in the Chiricahuas at least, that is quite like it. Through long-term population monitoring and close support from law enforcement personnel, state wildlife and federal land management agencies can ensure that Barfoot and its twinspots will continue to be an important part of Arizona's natural heritage.

ACKNOWLEDGMENTS

We were fortunate to have elicited support from many people during this project, and would like to express our deep gratitude to all involved. Kate Schoenecker provided excellent field assistance during 1997. Gary Helbing of the U.S. Forest Service enthusiastically provided project support. Greg Lelo, U.S. Forest Service, loaned us seismic sensors and Evert Herrick, Joint Counter Narcotics Task Force, and Bruce Haviland, U.S. Forest Service, assisted with their emplacement and concealment. Phil Young, National Park Service, and Dr. Paul Krausman, University of Arizona, loaned us cameras for surveillance. Chris Scott, Kim Murphy, Jeff Gee, Rob Danno, Steve Mazur, and Barney Tomberlin shared their insights regarding reptile poaching in the Chiricahuas. Steve DeStefano helped develop distance sampling protocols. Don DeYoung and Stephanie Cameron performed some of the snake surgeries and helped us procure surgical equipment. Cristina Jones, Caren Goldberg, and Erin Zylstra assisted with data analysis. George Bradley, Yar Petrysyn, Tom Huels, and Nina Johnson helped us identify prey items in fecal samples. Rosie Huerta and Carol Wakely provided vital administrative support.

Special thanks go to Andy Holycross, who donated not only his time, but his field personnel, equipment, and advice. We are also very grateful to the many other volunteers who braved cold, rainy weather, unstable rocks, and the risk of snakebite to make this project possible, including Marit Alanen, Heather Amrhein, Merryn Avent, Laurie and Roy Averill-Murray, Dan Bell, James Borgmeyer, Scott Breeden, Dennis Caldwell, Dawn Emmons, Brian Fedorko, Dan Fisher, Julia Fonseca, Ockie Fourie, Tiggy Grillo, Bryan Hamilton, Jeff Howland and family, Danny Kirk, Dave Larson, Jean-Francois LeGalliard, Carol Lutyk, Carlos Madden, Joe Martinez, Andrea and Todd McWhorter, Jack Oleile, April Osbourn, Mike Perkins, Phi Pham, Stephane Poulin, Laura Prival, Roger Repp, Ron Ryskalzc, Chris Scott, Jeff Servoss, Jesus Sigala, Lee Sloane, Lawrence Smith, Bryan Starrett, Eric Stitt, Debby Tipton, Andrea Tuijl, Thomas Tully, Dale Turner, Vince Walkosak, Mike Wall, Eric Wallace, and Chris Wolner. We apologize to anyone we have inadvertently omitted.

This study was funded by the Arizona Game and Fish Department Heritage Fund, T & E, Inc., and the University of Arizona Graduate Student Final Project Fund.

APPENDIX 1: MOUNTAIN SPINY LIZARD POPULATION DENSITIES

INTRODUCTION

We estimated the density of lizard populations at each site in order to quantify prey availability for *C. pricei*. Although bunch grass lizards (*Sceloporus scalaris*), striped plateau lizards (*Sceloporus virgatus*), and madrean alligator lizards (*Elgaria kingii*) were occasionally observed at our study sites, the most abundant lizard by far was the mountain spiny lizard (*Sceloporus jarrovii*). Therefore, our prey population estimates focused entirely on *S. jarrovii*. We used distance sampling to obtain these estimates (Buckland et al. 1993).

METHODS

The highly unstable nature of talus made a standard line transect system difficult to implement at our sites, as some attention had to be devoted to walking on the loose rock. We used a modified version of the point transect technique, which is often used to estimate population densities in areas where walking is difficult (Lancia et al. 1996).

We established single transects along lines about five meters from the upper and lower edges of the talus, as preliminary investigation revealed that mountain spiny lizards are observed in higher densities near edges. A transect was placed across the middle of two talus slopes to quantify the difference in lizard density in edge and non-edge areas. Each line was 250 m long. Along each line, 20 points were selected randomly (except where otherwise noted below) and marked with flagging.

Observers walked from flagged point to flagged point, stopping to observe at each point for one minute. The distance from each lizard observed to the nearest point was measured with a metric tape measure. Our technique differed from the standard point transect method because lizards observed while walking between points were also included. These lizards were treated the same way as lizards observed at points.

This modified sampling method does not appear to violate the assumptions for distance sampling (Buckland et al. 1993), but increases sample size because more lizards are observed. The same points were used more than once, but on different days. *Sceloporus jarrovii* are only active 2.5 days per week on average, so we believe it is likely that we counted different lizards on different days even from the same observation points (Simon and Middendorf 1976).

Barfoot was sampled in mid-September 1997 and late August 1998, Site 1 in late September 1997 and early September 1998, Site 2 in late September 1997 and mid-July, mid-August, and mid-September 1998, and Site 3 in mid-September 1998. All transects were run after the main parturition period for *S. jarrovii*. All transects were run in the absence of rain during hours when lizard activity was high, primarily in late morning and early afternoon.

Density estimates were calculated using Program DISTANCE (Laake et al. 1993). Following Buckland et al. (1993), data from each transect were truncated 10% prior to analysis. The best fitting model for each transect was used, either normal, hazard rate, or half-normal models.

A density index based on the number of lizards observed during each transect is also reported. To create the index, we standardized each transect run to 30 minutes of observation time (one minute of stationary observation at each point plus 30 seconds of walking observation between points). Due to the small size of the site, there were only 14 points in the Site 2 middle transect, so 21 minutes of observation time was assumed for that transect.

RESULTS

Highest *S. jarrovii* densities were detected along the edges of the Barfoot talus slopes (Table 4). In 1997, 65 lizards were observed during the survey, resulting in a density estimate of 260.9 lizards/ ha (SE = 62.9, 95% CI = 162.0 to 420.0). In 1998, the estimate increased to 527.0 lizards/ ha (SE = 81.3, 95% CI = 387.5 to 716.7) along the edges when 80 lizards were observed (Figure 12). The transects were located in different locations each year, which may have affected the results. Twenty lizards were observed during surveys across the middle of one of the talus slopes in 1998, resulting in a density estimate of only 21.6 lizards/ hectare (SE = 8.8, 95% CI = 9.8 to 47.8). The density index along the Barfoot edge was 1.08 lizards/ minute in 1997, and 0.89 lizards/ minute in 1998. Across the middle of the talus, the index was 0.22 lizards/ minute.

Table 4. Mountain spiny lizard density estimates

	Density Estimate 1997 (lizards/ ha)		Density Estimate 1998 (lizards/ ha)		Density Index 1997 (lizards/ minute)	Density Index 1998 (lizards/ minute)
	n	SE	n	SE		
Barfoot Edge	260.9	62.9	527.0	81.3	1.08	0.89
Barfoot Middle	-----	-----	21.6	8.8	-----	0.22
Site 1 Edge	177.9	77.3	32.8	17.5	0.66	0.12
Site 2 Edge	157.8	114.8	61.8	36.7	0.57	0.28
Site 2 Middle	-----	-----	43.3	81.3	-----	0.19
Site 3 Edge	-----	-----	92.1	46.3	-----	0.33

The next highest density of lizards was found along the slope edges at Site 1. However, the density decreased substantially between the years (Figure 13). In the first year, 59

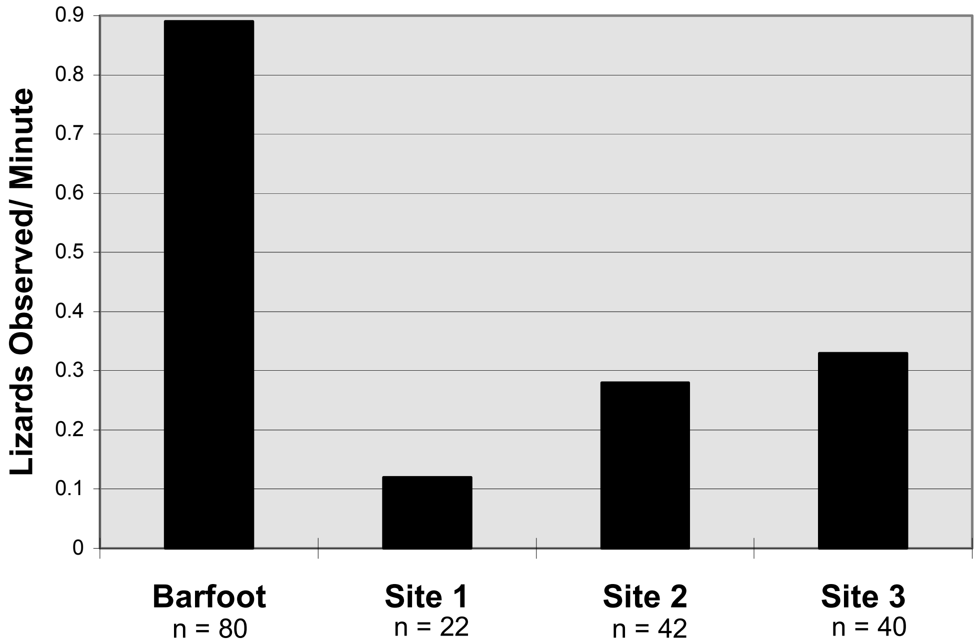

Figure 12. Mountain spiny lizard density indices - 1998

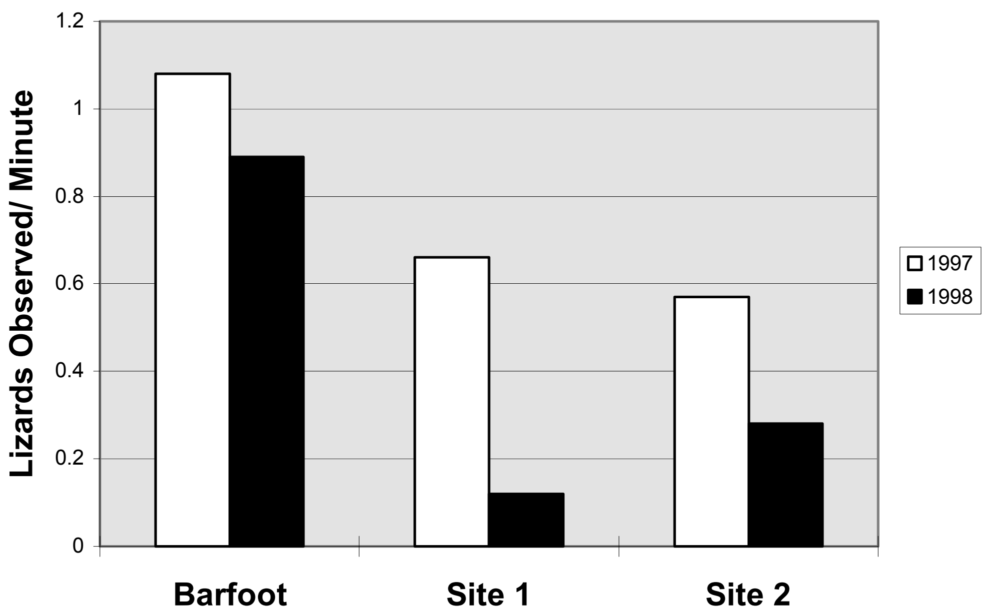

Figure 13. Yearly differences in mountain spiny lizard density indices

lizards were observed during the transects, resulting in a density estimate of 177.9 lizards/ hectare (SE = 77.3, 95% CI = 77.8 to 407.0). In the second year, only 22 lizards were seen and estimated density dropped to just 32.8 lizards/ hectare (SE = 17.5, 95% CI = 11.6 to 92.2). The index of density was 0.66 lizards/ minute in 1997, 0.12 lizards/ minute in 1998.

Site 2 also exhibited a sharp decline in *S. jarrovii* numbers between the two years. In 1997, with 34 lizards observed, we estimated 157.8 lizards/ hectare along the edge at the site (SE = 114.8, 95% CI = 42.1 to 591.1). In 1998, density estimates dropped to 61.8 lizards/ hectare (SE = 36.7, 95% CI = 20.5 to 186.5) when 42 lizards were observed but a greater number of transects were run. A transect across the middle of the talus at this site produced an estimate of 43.3 lizards/ hectare (SE = 81.3, 95% CI = 1.8 to 1018.2); eight lizards were seen. In addition to the large confidence interval for the latter estimate, it should be noted that Site 2 has a much larger edge: surface area ratio than Barfoot. The density index along the edges was 0.57 lizards/ minute in 1997, 0.28 in 1998, and 0.19 across the middle in 1998.

Lizard densities at Site 3 were only examined in 1998. The resulting estimate of 92.1 lizards/ hectare (SE = 46.3, 95% CI = 35.6 to 238.0), based on 40 lizard sightings, was higher than the 1998 estimates at Site 1 or Site 2. Only slope edges were sampled at this site. The index of density at the site was 0.33 lizards/ minute in 1998.

DISCUSSION

Based on both density estimate methods, Barfoot had the highest density of lizards during both years. This may explain the correspondingly high density of *C. pricei* at the site, as well as the preliminary indication that *C. pricei* home range may be smaller at Barfoot than at the other sites.

The data also confirm our observation that, on the larger talus slopes at least, *S. jarrovii* tend to be more concentrated along the slope edges than in the middle. We tended to find *C. pricei* near vegetation and along the slope edges more often than we found them in the middle of the large slopes. When our radiotelemetered snakes were on talus, they were rarely found more than 10 m from the edge (unless they were next to an island of talus vegetation), which may be related to the greater availability of lizard prey near the edges.

We observed a decline in lizard densities at Sites 1 and 2 between 1997 and 1998, and also at Barfoot if the density index is followed. Our radiotelemetered snakes were found on talus less often in 1998 than 1997, and perhaps *S. jarrovii* were less active on the talus in 1998 as well.

APPENDIX 2: POTENTIAL IMPACT OF TWIN-SPOTTED RATTLESNAKE COLLECTING ON MOUNTAIN SPINY LIZARDS

INTRODUCTION

Collecting has a direct effect on some lizards because *S. jarrovii* themselves are collected by people at Barfoot as feeder lizards and for the pet trade. In October 1979, one of us (CRS) observed four snake collectors capture approximately 200 *S. jarrovii* at Barfoot while they searched for *C. pricei*. The lizards were captured to feed the collectors' captive snakes in California.

Although we did not observe *S. jarrovii* collecting on this scale during our study, one individual was issued a citation by the wildlife manager for collecting four *S. jarrovii* without a hunting license at Barfoot. With a hunting license, individuals may legally collect four *S. jarrovii* per year or have four in possession (AGFD 1999). "Generalist" collectors likely seek both *C. pricei* and these lizards when at Barfoot, but no one knows how this collecting might affect the lizard population at the site.

Theoretically, the relatively high density of lizards at Barfoot could be a result of the removal of one of their main predators, *C. pricei*, from the site by collectors. We manipulated our population estimates and metabolic rate data from other studies to determine whether *C. pricei* could have a substantial impact on *S. jarrovii* abundance at the site.

METHODS

We estimated the abundance of *S. jarrovii* at Barfoot by using the population densities reported for 1998 in Appendix 1, assuming that lizard populations are at the "edge" density between 0 and 10 m from the edge, and at the "middle transect" density elsewhere on the slopes (Table 4). The circumference of the Barfoot talus slopes is about 1,930 m and the area is 3.1 ha.

To determine the number of lizards eaten by an average *C. pricei*, we estimated the average energy requirement of the snakes. We did not directly measure metabolic rate in *C. pricei*, but used published mass-related metabolic rate formulas for other rattlesnake species. Beaupre (1993) showed that mass accounts for virtually all of the difference in metabolic rates between rattlesnake species during his study of rock rattlesnakes (*Crotalus lepidus*) and blacktail rattlesnakes (*Crotalus molossus*) in southwestern Texas. Beck (1995) found that western diamondback rattlesnakes (*Crotalus atrox*), tiger rattlesnakes (*Crotalus tigris*), and blacktail rattlesnakes near Tucson, Arizona had similar metabolic rates to those reported for other crotalids, after correcting for mass.

The formula used to derive metabolic rate from mass is: $MR = aM^b$ (MR = metabolic rate, M = mass, a = mass coefficient, b = mass exponent) (Andrews and Pough 1985). Metabolic rates for rattlesnakes have only been reported at 15°C and 25°C. Therefore, for these calculations, we assumed that *C. pricei* have a body temperature of approximately 25°C from May to October between 0800 and 1800, and a body temperature of about 15°C the rest of the time. Under this assumption, *C. pricei* would have a body temperature of 25°C for 1,840 hours, and 15°C for 6,920 hours in one year.

Beck (1991) derived the following metabolic rate equations for resting rattlesnakes:
At T_{body} = 25°C, $MR = 0.0175M^{0.977}$

At T_{body} = 15°C, MR = $0.0193M^{0.793}$
We used these equations to generate O_2 consumption rates, which were then converted to energy by assuming a conversion factor of 1.124 J/ ml O_2 (Beck 1995). These figures were used to estimate the number of *S. jarrovii* required to fulfill the energy requirement of the Barfoot *C. pricei* population.

RESULTS

Average mass of *C. pricei* in our study was 53.8 g. Metabolic rates for *C. pricei* were therefore estimated as 0.859 ml O_2/ hour at 25°C and 0.455 ml O_2/ hour at 15°C. These metabolic rates are similar to those derived for *C. lepidus* individuals of the same mass (Beaupre 1993). The calculated energy consumption rate is 0.966 J/ hour at 25°C and 0.511 J/ hour at 15°C. Assuming the snakes spend 1,840 hours at 25°C and 6,920 hours at 15°C, the total energy requirement is 5.31 KJ/ year.

Measurements of 899 *S. jarrovii* in the Chiricahua Mountains between 1973 and 1978 resulted in an average mass estimate of 10.5 g (SE = 0.2) (Smith and Ballinger 1994). On average, ectotherms are able to assimilate about 50% of their prey (Pough et al. 1998). Mammalian prey has an energy content of about 0.30 KJ/g (Beck 1995). Assuming lizard prey has a similar energy content, a lizard represents roughly 3.15 KJ of energy, half of which (1.575 KJ) could be assimilated by snakes. Our diet analysis suggests that *Sceloporus* accounts for about 80% of the prey taken by twin-spotted rattlesnakes on talus. If these snakes obtain 80% of their energy from *S. jarrovii*, a *C. pricei* of average mass needs to eat only 2.7 lizards per year to obtain the 4.25 KJ of lizard energy needed to survive. In total, the equations imply that the snakes need to eat prey equivalent to only about 66% of their body mass each year.

We estimated that 1,043 *S. jarrovii* inhabit the Barfoot talus slopes, meaning that almost 11 kg of lizard prey are available. This translates to about 3,285 KJ of lizard prey energy of which snakes could assimilate 1,643 KJ. Earlier in this report, we estimated that there were 96 *C. pricei* at Barfoot. If they each ate the minimal number of lizards, they would remove 260 lizards from the population each year, almost 1/4 of the population - a substantial impact. Conversely, we find that there are enough lizards at Barfoot to support 387 twin-spotted rattlesnakes for one year. Hence, prey availability does not seem to be a limiting factor for the Barfoot snakes.

DISCUSSION

Obviously, we had to make numerous assumptions to arrive at these conclusions. We have probably underestimated the number of lizards eaten by twin-spotted rattlesnakes each year. The metabolic rate equations assume that the snakes are never active, which is not the case. Also, our body temperature data indicates that the snakes are often warmer than 25°C, and rarely do they get as cold as 15°C, so even their resting metabolic rates are higher than calculated.

Our data suggest, therefore, that *C. pricei* do in fact have a sizable impact on the population size of *S. jarrovii* at Barfoot. The removal of a large number of snakes would probably affect lizard abundance at the site. But do the snakes affect lizard density? There is evidence that food abundance has a significant impact on the size of *S. jarrovii* territories, which in turn would affect lizard density at the site (Simon 1975). The answer to whether or not *C. pricei* also plays a regulatory role will have to wait for some future experimental study.

LITERATURE CITED

Amaral, A. do. 1927. Studies of nearctic ophidia. Bulletin of the Antivenin Institute of America 1(2): 48-54.

Andrews, R.M. and F.H. Pough. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. Physiological Zoology 58: 214-231.

Arizona Game & Fish Department (AGFD). 1999. Arizona reptile & amphibian regulations. AGFD, Phoenix, Arizona.

Armstrong, B.L. and J.B. Murphy. 1979. The natural history of Mexican rattlesnakes. University of Kansas Publications, Lawrence, Kansas.

Beaupre, S.J. 1993. An ecological study of oxygen consumption in the mottled rock rattlesnake, *Crotalus lepidus lepidus*, and the black-tailed rattlesnake, *Crotalus molossus molossus*, from two populations. Physiological Zoology 66(3): 437-454.

Beck, D.D. 1991. Physiological and behavioral consequences of reptilian life in the slow lane: ecology of beaded lizards and rattlesnakes. Ph.D. Dissertation. University of Arizona.

Beck, D.D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. Journal of Herpetology 29(2): 211-223.

Behler, J.L., and F.W. King. 1979. National Audubon Society field guide to North American reptiles and amphibians. Alfred A. Knopf, Inc., New York.

Bennett, P.S., R.R. Johnson, and M.R. Kunzmann. 1996. An annotated list of vascular plants of the Chiricahua Mountains. U.S. Geological Survey, Tucson, Arizona.

Bowles, D. 1996. Wildlife trade - a conserver or exploiter? *In* V.J. Taylor and N. Dunstone (eds.). The exploitation of mammal populations. Chapman & Hall, London. pp.266-291.

Brazaitis, P. 1986. Reptile leather trade: the forensic science examiner's role in litigation and wildlife law enforcement. Journal of Forensic Sciences 31(2): 621-629.

Brown, D.E. (ed.). 1994. Biotic communities. University of Utah Press, Salt Lake City, Utah.

Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman & Hall, London.

Bullock, R.E. 1971. Cannibalism in captive rattlesnakes. Great Basin Naturalist 31(2): 49-50.

Campbell, J.A. and W.W. Lamar. 1989. The venomous reptiles of Latin America. Comstock Publishing Associates, Ithaca, New York.

Congdon, J.D., R.E. Ballinger, and K.A. Nagy. 1979. Energetics, temperature, and water relations in winter aggregated *Sceloporus jarrovi* (Sauria: Iguanidae). Ecology 60(1): 30-35.

Cordero, G.A. and J. Ohasti. 1981. Comparison of capybara populations of open and forested habitats. Journal of Wildlife Management 45(1): 267-271.

Cunningham, J.D. 1959. Reproduction and food of some California snakes. Herpetologica 15: 17-19.

Dodd, C.K., Jr. 1987. Status, conservation, and management. *In* R.A. Seigel, J.T. Collins, and S.S. Novak (eds.). Snakes: ecology and evolutionary biology. McGraw Hill, Inc., New York. pp. 478-513.

Dodd, C.K., Jr. 1993. Strategies for snake conservation. *In* R.A. Seigel and J.T. Collins (eds.). Snakes: ecology and behavior. McGraw-Hill, Inc., New York. pp. 363-393.

Du Bray, E.A., D.B. Yager, and J.S. Pallister. 1992. Rustler Park Quadrangle, Cochise County, Arizona - analytic data and geologic sample catalog. U.S. Geological Survey, Denver, Colorado.

Elgar, M.A. and B.J. Crespi. 1992. Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford, England.

Ernst, C.H. 1992. Venomous reptiles of North America. Smithsonian Institution Press, Washington, D.C.
Fitzgerald, S. 1989. International wildlife trade: whose business is it? World Wildlife Fund, Washington, D.C.
Funk, R.S. 1965. Food of *Crotalus cerastes laterorepens* in Yuma County, Arizona. Herpetologica 21(1): 15-17.
Geist, V. 1994. Wildlife conservation as wealth. Nature 368: 491-492.
Genter, D.L. 1984. *Crotalus viridis* (prairie rattlesnake) - food. Herpetological Review 15(2): 49-50.
Gloyd, H.K. 1933. An unusual feeding record for the prairie rattlesnake. Copeia 1933(2): 98.
Gloyd, H.K. 1937. A herpetological consideration of faunal areas in southern Arizona. Bulletin of the Chicago Academy of Sciences 5(5): 79-136.
Gloyd, H.K. 1940. The rattlesnakes, genera *Sistrurus* and *Crotalus*: a study in zoogeography and evolution. Special Publication No. 4., The Chicago Academy of Sciences, Chicago, Illinois.
Goode, M.J., D.E. Swann, C.R. Schwalbe, and R.W. Mannan. 1998. The effects of microhabitat destruction on reptile abundance. Arizona Game & Fish Department, Phoenix, Arizona.
Groombridge, B. (ed.). 1992. Global biodiversity: status of the earth's living resources. Chapman & Hall, London.
Gumbart, T.C. and K.A. Sullivan. 1990. Predation on yellow-eyed junco nestlings by twin-spotted rattlesnakes. The Southwestern Naturalist 35(3): 367-368.
Harris, H.S., Jr. and R.S. Simmons. 1977. Additional notes concerning cannibalism in pit vipers. Bulletin of the Maryland Herpetological Society 13(2): 121-122.
Hathcock, B. 1937. Snake eat snake. Natural History 39(5): 339-342.
Hemley, G. (ed.). 1994. International wildlife trade: a CITES sourcebook. Island Press, Washington, D.C.
Herrera, E.A. 1992. The effect of harvesting on the age structure and body size of a capybara population. Ecotropicos 5(1): 20-25.
Hoser, R. 1992. Smuggled: the underground trade in Australia's wildlife. Apollo Books, Sydney, Australia.
International Union for Conservation of Nature and Natural Resources (IUCN). 1980. World conservation strategy. IUCN, Gland, Switzerland.
Jester, S.L, C.E. Adams, and J.K. Thomas. 1990. Commercial trade in Texas nongame wildlife. Texas Parks & Wildlife Department, Austin, Texas.
Joanen, T., L. McNease, R.M. Elsey, and M.A. Staton. 1997. The commercial consumptive use of the American alligator (*Alligator mississippiensis*) in Louisiana: its effects on conservation. *In* C.H. Freese (ed.). Harvesting wild species: implications for biodiversity conservation. The Johns Hopkins University Press, Baltimore, Maryland. pp. 465-506.
Johnson, T.B. and G.S. Mills. 1982. A preliminary report on the status of *Crotalus lepidus*, *C. pricei*, and *C. willardi* in southeastern Arizona. U.S. Fish & Wildlife Service.
Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225-247.
Kauffeld, C. 1943a. Field notes on some Arizona reptiles and amphibians. American Midland Naturalist 29(2): 342-359.
Kauffeld, C. 1943b. Growth and feeding of new-born Price's and green rock rattlesnakes. American Midland Naturalist 29(3): 607-614.
Kauffeld, C. 1957. Snakes and snake hunting. Hanover House, Garden City, New York.
Kauffeld, C. 1969. Snakes: the keeper and the kept. Doubleday & Co., Inc., Garden City, New York.

Keasey, M.S., III. 1969. Some records of reptiles at the Arizona-Sonora Desert Museum. International Zoo Yearbook 9: 16-17.
Klauber, L.M. 1936. A key to the rattlesnakes with summary of characteristics. Transactions of the San Diego Society of Natural History 8(20): 185-276.
Klauber, L.M. 1972. Rattlesnakes: their habits, life histories, and influence on mankind. 2nd ed. University of California Press, Berkeley, California.
Laake, J.L., S.T. Buckland, D.R. Anderson, and K.P. Burnham. 1993. DISTANCE User's Guide. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado.
Lancia, R.A., J.D. Nichols, and K.H. Pollock. 1996. Estimating the number of animals in wildlife populations. *In* T.A. Bookhout (ed.). Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland. pp. 215-253.
Lillywhite, H.B. 1982. Cannibalistic carrion ingestion by the rattlesnake, *Crotalus viridis*. Journal of Herpetology 16(1): 95.
Lowe, C.H. 1964. The vertebrates of Arizona. University of Arizona Press, Tucson, Arizona.
Lowe, C.H., C.R. Schwalbe, and T.B. Johnson. 1986. The venomous reptiles of Arizona. Arizona Game and Fish Department, Phoenix, Arizona.
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(1): 61-73.
Mahaney, P.A. 1997a. *Crotalus pricei* - reproduction. Herpetological Review 28(7): 205.
Mahaney, P.A. 1997b. Taxon management account: twin-spotted rattlesnake *Crotalus pricei* ssp. Arizona-Sonora Desert Museum, Tucson, Arizona.
Malik, S., P.J. Wilson, R.J. Smith, D.M. Lavigne, and B.N. White. 1997. Pinniped penises in trade: a molecular-genetic investigation. Conservation Biology 11(6): 1365-1374.
Matthiessen, P. 1987. Wildlife in America. 2nd ed. Penguin Books, New York.
Martin, B. 1974. Distribution and habitat adaptations in rattlesnakes of Arizona. Bulletin of the New York Herpetological Society 10(3&4): 3-12.
McCranie, J.R. and L.D. Wilson. 1987. The biogeography of the herpetofauna of the pine-oak woodlands of the Sierra Madre Occidental of Mexico. Milwaukee Public Museum Contributions in Biology and Geology, no. 72.
McCrystal, H.K., C.R. Schwalbe, and D.F. Retes. 1996. Selected aspects of the ecology of the Arizona ridge-nosed rattlesnake (*Crotalus willardi willardi*) and the banded rock rattlesnake (*Crotalus lepidus klauberi*) in Arizona. Arizona Game & Fish Department, Phoenix, Arizona.
Mitchell, J.C. 1986. Cannibalism in reptiles: a worldwide review. Herpetological Circular No. 15, Society for the Study of Amphibians and Reptiles.
National Weather Service. 1999. http://nimbo.wrh.noaa.gov/Tucson/twc.html
Neill, W.T. 1961. Giant rattlesnakes: past and present. Florida Wildlife 15(1): 10-13.
Polis, G.A. and C.A. Myers. 1985. A survey of intraspecific predation among reptiles and amphibians. Journal of Herpetology 19(1): 99-107.
Porter, T. 1983. Induced cannibalism in *Crotalus mitchellii*. Bulletin of the Chicago Herpetological Society 18(2): 48.
Potten, C.J. 1991. America's illegal wildlife trade: a shameful harvest. National Geographic 180(3): 106-132.
Pough, F.H., R.M. Andrews, J.E. Cadle, M.L. Crump, A.H. Savitzky, and K.D. Wells. 1998. Herpetology. Prentice-Hall, Inc., Upper Saddle River, New Jersey.
Powers, A. 1972. An instance of cannibalism in captive *Crotalus viridis helleri* with a brief review of cannibalism in rattlesnakes. Bulletin of the Maryland Herpetological Society 8(3): 60-61.

Primack, R.B. 1998. Essentials of conservation biology. 2nd ed. Sinauer Associates, Sunderland, Massachusetts.
Rubio, M. 1992. In the footsteps of Carl Kauffeld. Sonoran Herpetologist 5(7): 64-69.
Rubio, M. 1998. Rattlesnake: portrait of a predator. Smithsonian Institution Press, Washington, D.C.
Ruby, D.E. 1977. Winter activity in Yarrow's spiny lizard, *Sceloporus jarrovi*. Herpetologica 33: 322-333.
Ruthven, A.G. 1911. A biological survey of the sand dune region on the south shore of Saginaw Bay, Michigan, amphibians and reptiles. Michigan Geological and Biological Survey, Publication no. 4, Biological Series 2: 257-272.
Scott, C. 1996. Uncovering the business of reptiles. The Florida Naturalist. Summer: 20-21.
Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika 52: 249-259.
Seigel, R.A. and N.B. Ford. 1992. Effect of energy input on variation in clutch size and offspring size in a viviparous reptile. Functional Ecology 6: 382-385.
Simon, C.A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology 56: 993-998.
Simon, C.A. and G.A. Middendorf. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. Ecology 57: 1317-1320.
Smith, G.R. and R.E. Ballinger. 1994. Temperature relationships in the high-altitude viviparous lizard, *Sceloporus jarrovi*. American Midland Naturalist 131: 181-189.
Smith, H.M. 1946. Preliminary notes and speculations on the *Triseriatus* group of rattlesnakes in Mexico. The University of Kansas Science Bulletin 31(3): 75-101.
Snider, A.T. and J.K. Bowler. 1992. Longevity of reptiles and amphibians in North American collections. 2nd ed. Society for the Study of Amphibians and Reptiles.
Stebbins, R.C. 1985. A field guide to western reptiles and amphibians. 2nd ed. Houghton Mifflin Co., Boston.
Swanson, T.M. 1992. Wildlife and wildlands, diversity and development. *In* T.M. Swanson and E.B. Barbier (eds.). Economics for the wilds. Earthscan Publications Limited, London. pp. 1-14.
Tanner, W.W. 1985. Snakes of western Chihuahua. Great Basin Naturalist 45: 615-676.
Thapar, V. 1996. The tiger - road to extinction. *In* V.J. Taylor and N. Dunstone (eds.). The exploitation of mammal populations. Chapman & Hall, London. pp.292-301.
Tweit, S.J. 1997. Going, going...gone? Sonoran Herpetologist 10(5): 50-52.
United States Forest Service (USFS). 1986. Draft environmental impact statement, proposed Mt. Graham Astrophysical Area, Pinaleno Mountains, Coronado National Forest. USFS, Tucson, Arizona.
Van Biema, D. 1994. The killing fields. Time. 22 August: 36-37.
Van Denburgh, J. 1895. Description of a new rattlesnake (*Crotalus pricei*) from Arizona. Proceedings of the California Academy of Sciences 2(5): 856-857.
Van Denburgh, J. 1896. A list of some reptiles from southeastern Arizona, with a description of a new species of *Cnemidophorus*. Proceedings of the California Academy of Sciences 2(6): 338-349.
Van Denburgh, J. 1922. The reptiles of western North America. California Academy of Sciences, San Francisco, California.
Van Devender, T.R. and C.H. Lowe. 1977. Amphibians and reptiles of Yepómera, Chihuahua, Mexico. Journal of Herpetology 11(1): 41-50.
Webster, D. 1997. The looting and smuggling and fencing and hoarding of impossibly precious, feathered and scaly wild things. The New York Times Magazine. February 16. pp. 26-33, 48-49, 53, 61.
White, G. 1999. http://www.cnr.colostate.edu/~gwhite/mark/mark.htm

Wilkinson, T. 1996. Reptile rustlers. National Parks and Conservation 70: 36-39.
Williams, T. 1999. The terrible turtle trade. Audubon. March-April: 44-51.
Williamson, M.A. 1971. An instance of cannibalism in *Crotalus lepidus* (Serpentes: Crotalidae). Herpetological Review 3(1): 18.
Williamson, M.A. 1986. Trail of the snake. Sunstone Press, Santa Fe, New Mexico.
Wittig, A.S. 1998. Environmental thieves. Southeastern Arizona Magazine 2(5): 10-13.
Woodin, W.H. 1953. Notes on some reptiles from the Huachuca area of southeastern Arizona. Bulletin of the Chicago Academy of Sciences 9(15): 285-296.
Wright, A.H. and A.A. Wright. 1957. Handbook of snakes of the United States and Canada. Comstock Publishing Associates, Ithaca, New York.