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**Effects and Effectiveness of Rattlesnake Relocation
at Montezuma Castle National Monument**

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INTRODUCTION

The 1916 National Park Service Organic Act states, in part, that the purpose of the national parks is to "conserve the scenery and natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (National Park Service 1981). However, the presence of potentially dangerous resident wildlife in many national parks, including at least 12 species of rattlesnakes in the southwest (Stebbins 1985), complicates compliance with this mandate. The potential for a life-threatening snakebite to a visitor is a safety concern for many park managers, but they must also protect park rattlesnake populations. This issue is specifically referred to in Park Service management documents such as NPS-77: Natural Re-

sources Management Guidelines (1991), but despite a directive to manage potentially hazardous wildlife based on "scientific research and planning that . . . will protect the resources within parks in an effective and ecologically sound manner," very little scientific research has been conducted to address the issue of rattlesnake interactions with humans in park areas (but see Graham 1991, 1994).

Consequently, different parks have developed their own ad hoc policies for decreasing human-rattlesnake encounters. In 1994, we conducted a phone survey of rattlesnake management policies in 26 national parks and monuments throughout the southwestern United States (Table 1). In parks where the potential for snakebite is considered a management problem, a majority relocate "nuisance" rattlesnakes away from visitor and staff use

Table 1. Results of telephone survey of southwestern National Park Service rattlesnake management policies conducted in December 1993, based on interviews with resource managers, and superintendents. "Average # Nuisance Snakes Seen Per Year" is the average number of rattlesnakes deemed to be a hazard to human safety, generally those seen in visitor access or staff housing areas. Relocation distance of nuisance rattlesnakes and management policies, if any, are noted under "Management Policy, and "IPM" refers to Integrated Pest Management. "# of Recent Snake Bites" is the total number of rattlesnake bites in recent memory, based on written records or recollections of park staff, and generally refers to the period between 1980 and 1993, unless otherwise noted.

| PARK | AVG # NUISANCE SNAKES SEEN/YR | MANAGEMENT POLICY | # OF RECENT SNAKE BITES |
|--|----------------------------------|--|----------------------------|
| Arches N.P. (UT) | 4-5 | Relocation: < 0.5 km in direction of travel | 0 |
| Bandelier N.M. (NM) | 6 | Relocation: 100-200 m | 2 |
| Big Bend N.P. (TX) | 15-20 | Relocation: 2-5 km on request | 2 (last 6 yrs) |
| Canyon De Chelly N.M. (AZ) | ? | Relocation: 2-40 km or extermination | 0 |
| Canyonlands N.P. (UT) | 15-20 | Relocation: < 100 m. Written policy | 1 |
| Capitol Reef N.P. (UT) | 0 | None | 0 |
| Casa Grande N.M. (AZ) | 8-9 | Relocation on request: 100-200 m; follow IPM guidelines | 0 |
| Chaco Culture N.H.P. (NM) | 6 | Relocation: 100 m-2 km | 0 |
| Chiricahua N.M. / Fort Bowie N.H.S. (AZ) | 12 | Relocation to same habitat: 2-4 km. Written policy | 0 |
| Colorado N.M. (CO) | 0-1 | Relocation: < 1 km | 0 |
| Coronado N.M. (AZ) | 6 | Relocation: < 2 km | 0 |
| Death Valley N.P. (CA) | 0 | Follow IPM guidelines | 1 |
| Dinosaur N.M. (CO) | 0 to few | Relocation: 100-200 m | 0 |
| Grand Canyon N.P. (AZ) | 0 to few | Follow IPM guidelines and occasional relocation: < 8 km | avg 1/ every 2-3 yrs |
| Great Basin N.P. (NV) | 1-2 | Relocation to same habitat: < 5 km | 0 |
| Joshua Tree N.P. (CA) | 2-3 | Relocation: 100 m-0.5 km | 3 (last 5 yrs) |
| Mesa Verde N.P. (CO) | 6-8 | Relocation: 0.75-2.5 km | 0 |
| Montezuma Castle N.M. (AZ) | 12 | Relocation: < 2 km (developing written policy) | 1 |
| Natural Bridges N.M. (UT) | 15 | Relocation in direction of travel: < 200 m. Written policy | 1 |
| Organ Pipe Cactus N.P. (AZ) | 10-20 | Relocation: 2-4 km (developing written policy) | 0 |
| Pecos N.H.P. (NM) | 25 | Relocation: < 0.5 km | 0 |
| Petrified Forest N.P. (AZ) | 0-1 | None | 1 |
| Saguaro N.P. (AZ) | 5-6 | Relocation: < 2 km | 1 |
| Tonto N.M. (AZ) | 20-30 | Relocation: 150-300 m | 0 |
| Wupatki N.M. (AZ) | 6 | Relocation: 5 km (to backcountry) | 0 |
| Yucca House N.M. (CO) | 10-15 | Relocation ? | 1 |
| Zion N.P. (UT) | 12-20 | Relocation: 100-200 m | 0 |

areas, over distances varying from a few meters to 40 kilometers.¹

Relocation of nuisance animals from areas where they conflict with humans is a standard procedure used to manage a variety of species, including grizzly bears (Blanchard and Knight 1995), white-tailed deer (Jones et al. 1997), ground squirrels (Van Vuren et al. 1997), as well as rattlesnakes (Hare and McNally 1997, McNally 1995, Perry-Richardson and Ivanyi 1992). While there is little question that removing a nuisance animal from an area of contact with humans will mitigate the immediate threat, the resulting effects on the relocated animal must also be taken into consideration. Many studies of relocation have shown negative impacts on displaced animals, including increased wandering, aberrant social behavior, and increased mortality rates (Compton et al. 1995, Macmillan 1995, Moriarty and Linck 1995, Reinert and Rupert 1995, Bright and Morris 1994, Hambler 1994, Lloyd and Powlesland 1994, and see reviews of earlier work by Burke 1991, Dodd and Seigel 1991, and Reinert 1991).

Several unique aspects of rattlesnake life history suggest that rattlesnake survival, growth, and reproduction may be negatively impacted by relocation outside their normal activity (home) range. Successful hibernation in rock caves, crevices, burrows, or tree stumps is critical to rattlesnake survival in climates with freezing winter temperatures (Means 1977). Because hibernacula having suitable thermal and physical attributes are limited (Sexton et al. 1992, Gregory 1984), rattlesnakes that are relocated to areas that do not contain suitable hibernacula (and perhaps those relocated just before hibernation) have high rates of mortality due to exposure to freezing temperatures and/or predation (e.g. Johnson 1996).

Displacement may also affect the reproductive success of rattlesnakes. In some regions, gravid females aggregate near preferred hibernacula in "rookeries" that have favorable thermal properties for optimal development of embryos, and that also provide protection from predators (Graves et al. 1986, King and Duvall 1990, Reinert and Zappalorti 1988b). If relocated during gestation to areas that do not contain suitable rookeries, females might have smaller litters with reduced survival of the remaining young, and might also suffer increased risks of predation. Many newborn rattlesnakes find suitable hibernacula in the fall by following pheromone trails emitted by adults during fall migration (Reinert and Zappalorti 1988a, Ford 1986, Graves et al. 1986). The young of a gravid female displaced into unsuitable habitat prior to parturition might also have a greatly increased chance of not finding suitable hibernacula.

Rattlesnakes relocated more than a few meters by public land managers are generally released into a few "favorite" locations (J. McNally, pers. comm.). The stress associated with repeated relocations of rattlesnakes into certain small areas could facilitate disease transmission and negatively impact the growth, survival, social structure, and genetic fitness of animals already inhabiting that area (Cunningham 1996, Wolf et al. 1996, McNally 1995, Davidson and Nettles 1992, Dodd and Seigel 1991, Reinert 1991).

Earlier studies of the effects of relocation on rattlesnakes has shown impacts on movement patterns, mortality rates, and social behavior. Some relocated adult rattlesnakes traveled in straight-line distances away from the release point until they were lost, and/or exhibited aberrant social behavior (Reinert and Rupert 1995, Galligan and Dunson 1979, Landreth 1973, Fitch and Shirer 1971). Many relocated rattlesnakes also have greatly increased mortality rates (Hare and McNally 1997, Johnson 1996, McNally 1995, Reinert and Rupert 1995). To date, however, no studies have examined the effects and effectiveness of rattlesnake relocation as a management technique in national parks.

The potential for human-rattlesnake interactions is particularly great at the Castle Unit of Montezuma Castle National Monument in central-north Arizona. This area receives approximately 900,000 visitors each year, and about 12 rattlesnake sightings (western diamondbacks [*Crotalus atrox*] and black-tailed rattlesnakes [*C. molossus*]) occur around visitor areas and staff housing each year (S. Sandell, pers. comm.). Prior to 1994, due to the high number of nuisance rattlesnakes sighted and to an envenomation in the 1980's, at least 75% of nuisance rattlesnakes were removed from the monument to adjacent National Forest Service land.

To examine the effects of relocation on rattlesnakes and the effectiveness of relocation as a management technique at the monument, we developed the following objectives: 1) Determine location of rattlesnake hibernacula and summer foraging areas; 2) Determine the reasons for rattlesnake presence in visitor use areas; 3) Compare the behavior, activity range size, movement patterns, indices of condition, and mortality rates of rattlesnakes that are experimentally relocated to control snakes that are not relocated (i.e. snakes that are left in their original activity range); 4) Determine the homing ability of snakes relocated outside of their "normal" activity range; and 5) Assess the effectiveness of rattlesnake relocation as a management tool. Based on the results of these objectives, we developed guidelines for rattlesnake management at the monument.

¹ The variation in relocation distances is not due to scientific comparison of various relocation distances, but rather to differing amounts of human use areas in parks, and to differing staff attitudes about the inherent hazard posed by rattlesnakes.

MATERIALS AND METHODS

Site

Montezuma Castle National Monument is located in the Verde Valley of north-central Arizona at approximately 3800' (1158 m) elevation (Figure 1, page 4). We conducted this study at and adjacent to the 580-acre Castle unit, which is bordered to the north, east and south by United States Forest Service land, and to the west by Interstate 17. This area is bisected by a perennial stream (Wet Beaver Creek) that contains sections of subsurface water flow and has riparian vegetation characteristic of Sonoran Riparian Deciduous Forest Scrubland (Minckley and Brown 1994). Upland vegetative communities in the area are dominated by the Creosotebush-Crucifixion-thorn Series of the Arizona Upland Division of the Sonoran Desertscrub, but vegetation representative of the Chihuahuan, Mohave, and Great Basin Desertscrubs is also present (Turner and Brown 1994). The region also contains many porous limestone outcrops and cliffs.

MATERIALS

We used temperature-sensing implantable radio transmitters from Telonics Telemetry-Electronics Consultants (Mesa, Arizona) and Holohil Systems, Ltd. (Ontario, Canada). Transmitters ranged in weight from 11.0 to 13.8 grams, and transmitting life was approximately 12 months for Telonics and 24 months for Holohil models. Snakes were located with a Telonics model TR-4 receiver and "H"-style directional antenna. We used a Trimble Navigation (Sunnyvale, California) Geo-Explorer global positioning system (GPS) unit and Pathfinder software to record these locations.

GENERAL METHODS

Western diamondbacks (*Crotalus atrox*) and black-tailed rattlesnakes (*Crotalus molossus*) at Montezuma Castle were captured opportunistically between 1 June 1994 and 1 December 1996. All were restrained in plastic tubes, weighed, measured (snout-vent and tail length), and sexed. The rattlesnakes were painted on the basal three rattles with individual color combinations using semi-permanent Testor's model paint, and after processing released near their capture sites. Each animal was subsequently identified by either the color combination (e.g., Go-Si-Blk: Gold-Silver-Black) or, if implanted with a radio-transmitter, by an individual receiver channel number (e.g., Channel 34).

Starting in August 1994, 19 adult western diamondbacks (10 males and nine non-pregnant females, large enough so that a transmitter would be less than five percent of their body weight) were held for transmitter implantation. We followed the implantation procedures of Greene and Hardy (1992 unpubl., after Reinert 1992) unless otherwise indicated. Eligible rattlesnakes were anesthetized in a specialized aquarium setup using gaseous isoflurane

at a veterinary hospital. Anesthesia was administered by tracheal intubation during surgery, and the lungs artificially inflated during and after surgery to ensure adequate anesthesia and oxygen. Veterinarians followed sterile surgical procedure to implant a radio-transmitter in the coelomic cavity of each rattlesnake about 2/3 of the snout-vent length behind the head, extending the antenna subcutaneously toward the head. After surgery, each snake was given an injection of saline equal to at least five percent of its body weight to help prevent dehydration, and several animals with obvious wounds or infections were given a small dose of Amikacin antibiotic. All rattlesnakes were held in a quiet heated room for at least twelve hours to ensure adequate recovery from anesthesia, and were provided with water ad libitum.

After recovery, we returned all snakes to their original capture area and recorded their positions once every few days during their active period (generally, mid-March to mid-October) to ascertain movement patterns within their original activity range. We also located all rattlesnakes about once every two weeks during hibernation. When a snake was located, we recorded the time and date, air and substrate temperature, body temperature, microhabitat association, and behavior. We used a GPS unit to record exact positions of the snakes in universal trans-mercators (UTMs). We recaptured, weighed, and measured implanted snakes just after egress from hibernation, once during mid-summer, and just prior to hibernation to assess their condition and determine growth and weight change patterns. Additionally, several snakes had to be recaptured to implant new transmitters.

EXPERIMENTAL RELOCATION

By mid-August 1995, we had implanted eight adult western diamondbacks and had been tracking all for at least two weeks. Over a two-day period, four of these snakes (three males and one female) were selected at random (after stratifying for sex), placed in separate opaque five-gallon snake buckets, and hand-carried to separate relocation sites two kilometers east of the visitor center on U.S. Forest Service land (Figure 2, page 5). This relocation distance was twice as far as any snake had been observed to move in a straight-line distance during one active season up to that point. Relocation sites were chosen using a stratified random sampling procedure to place the snakes at least 0.5 kilometers apart from each other in habitat contiguous with the monument that did not contain developed communities, roads, and/or heavily-used recreation areas. The snakes were observed from a distance of at least 30 meters with binoculars for several hours after relocation to document immediate behavioral reactions.

At the same time, the remaining four rattlesnakes (three males and one female) were placed in opaque snake buckets, carried a distance equivalent to two kilometers, and then re-released at their latest capture points on the monument. These non-relocated

Rattlesnake Study Area Aug. 1994 - Dec. 1996

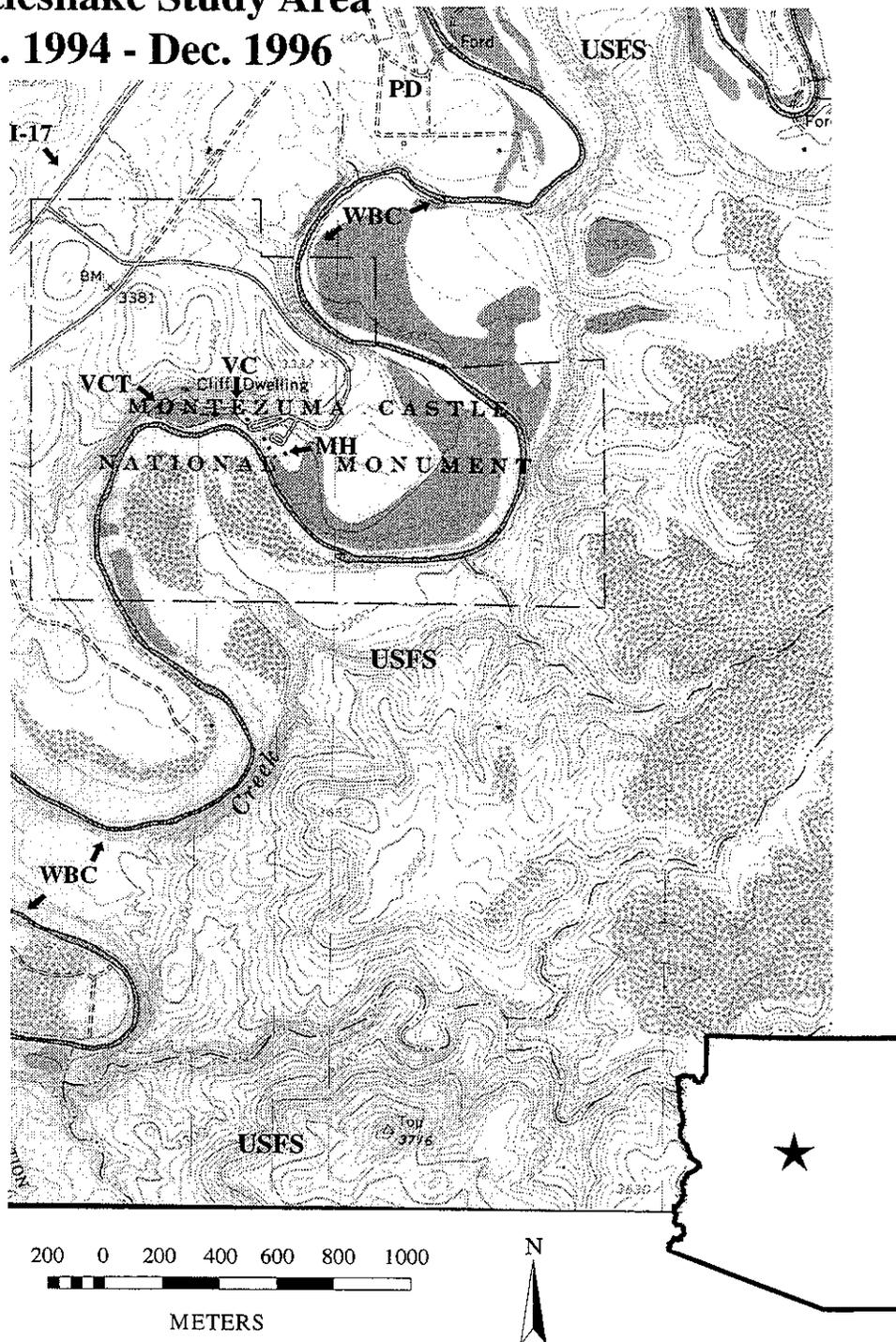
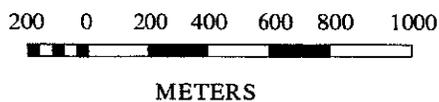
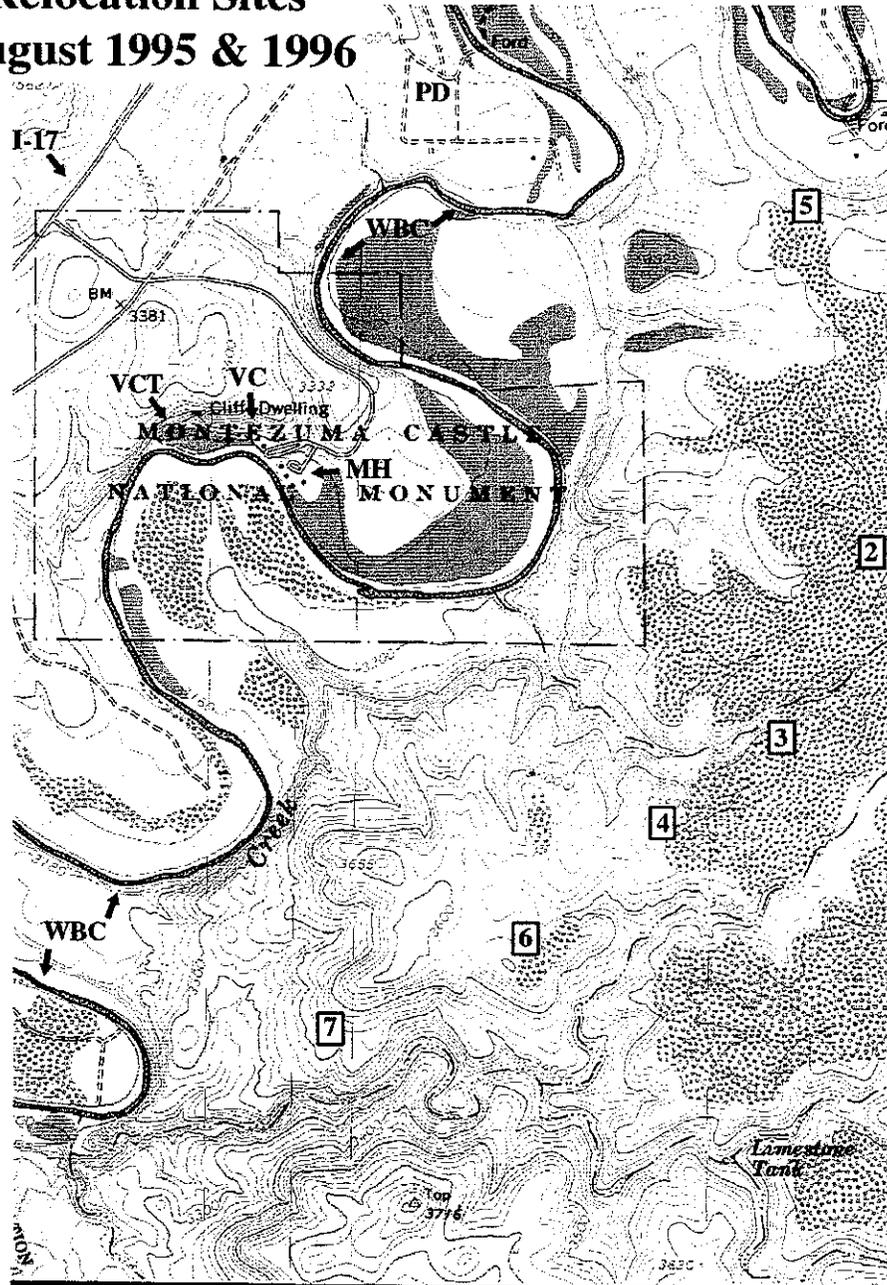


Figure 1. Location of experimental relocation study of western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, between August 1994 and December 1996, showing Monument location, topography, roadways, streams, and manmade features. Star within outline of Arizona shows relative position of study area in the state. I-17 = Interstate 17, MH = Monument housing area, PD = private developed area, USFS = U.S. Forest Service property, VC = Monument visitor center, VCT = visitor center area trails, WBC = Wet Beaver Creek.

Relocation Sites August 1995 & 1996



1 Individual Rattlesnake
Relocation Sites



Figure 2. Location of relocation sites on U.S. Forest Service land for seven western diamondback rattlesnakes, each at two km from Montezuma Castle National Monument, Arizona. Channels 25, 34, 41, and 23 were relocated to Sites 1, 2, 3, and 4, respectively, in August 1995; Channels 43, 29, and 16 were relocated to Sites 5, 6, and 7, respectively, in August 1996 (see Methods for experiment description). I-17 = Interstate 17, MH = Monument housing area, PD = private developed area, VC = Monument visitor center, VCT = visitor center area trails, WBC = Wet Beaver Creek.

snakes provided a control for any effect of handling of the physically relocated animals, and are henceforth referred to as "control" snakes.

We repeated this experiment in mid-August 1996 with six rattlesnakes not previously involved in the experiment: one female and two males were relocated, while one female and two males acted as controls. In 1996, neither control nor relocated rattlesnakes were observed immediately after their release due to suspected observer and/or handling effects on the snakes noted during the previous year.

DATA ANALYSES

General

For all data analyses, snakes lost prior to experimental treatment ("non-experimental snakes") were excluded. We determined the effects of relocation by comparing WITHIN treatment group (i.e., control or relocated snakes) before and after the relocation experiment using paired-t-tests; and by comparing BETWEEN treatment groups before or after the experiment using independent-samples t-tests (Sokal and Rohlf 1981). For each parameter, we also examined extra-experimental effects, including year of the study, sex of the animal, and season of year (for movement data only). Relocated snakes after treatment were excluded from this second type of analysis.

All data were analyzed using the statistical computer program SPSS ver. 7.0 (1996). For all parametric data analysis, we log-transformed non-normally distributed data, and used Levene's test of homogeneity of variance to verify that variances between groups were homogenous (Neter et al. 1990). Means are reported followed by \pm one standard deviation. Frequency data were analyzed using the Chi-square test with the Pearson estimator of X^2 (Sokal and Rohlf 1981). Within-group comparisons of frequency data were made using the non-parametric Wilcoxon Matched-Pairs Signed-Rank test, and between-group comparisons were made with the Mann-Whitney-U - Wilcoxon Two-Sample test (Sokal and Rohlf 1981). Significance was determined at the $p \leq 0.05$ level.

Activity (Home) Range

Rattlesnake locations, movement patterns and activity ranges were mapped using Pathfinder, ARC-Info, and ARC-View mapping programs. To estimate the activity range size for each snake, we used the minimum convex polygon method (White and Garrott 1990) in the computer program Telem (K. McKelvey, pers. comm.). Because the size of the activity range of any animal is largely dependent on the number of its locations (Reinert 1992), the data were standardized: to compare activity range sizes between the relocated and control groups, and to determine extra-experimental effects, we included only snakes for which we had at least two months of data prior to the experiment. To compare the range size of each snake before and after treatment, we standardized the range data for each snake by comparing the shortest number of weeks immediately preceding or following the experiment (e.g., if a snake was tracked for eight weeks before the experiment

and twenty weeks after, we compared the eight weeks before with only the eight weeks immediately after the experiment).

Movement Patterns

To determine if there were changes in movement patterns of the snakes resulting from the relocation experiment, the following indices were calculated: 1) average distance moved per day (in meters); 2) frequency of movement between consecutive locations; 3) total number of new locations used divided by total locations used; 4) total distance traveled from the release site at the time of the experiment to the hibernation location first used after the experiment; and 5) directionality of movements between consecutive locations. These parameters were calculated solely as indices of movement and are not intended to be precise descriptions of actual movement patterns made by the snakes. To standardize these data, we set the following conditions: a movement was defined as any distance between successive locations greater than six meters; and for parameters 1) and 2) above, any successive locations more than four days apart (likely for the snake to have moved due solely to time elapsed) were excluded. We also analyzed movement data by season, defined as: spring: March and April; dry summer: May- June (prior to monsoonal activity); wet summer: July and September (during monsoons); and fall: September and October. Relocated snakes after the experiment were excluded from this analysis.

Average distance moved per day was calculated by dividing the distance between successive locations by the number of days between successive locations, for both the active season and the hibernation period. There was not enough information on hibernating relocated snakes before the experiment to calculate the average distance moved per day during hibernation, so these data were analyzed without that group, using a one-way ANOVA test (Neter et al 1990). To determine total distance traveled after the experimental release site to the first hibernation site, the distances between successive locations were summed. To determine the frequency of movement, the total number of movements of each snake was divided by the total number of its locations. To determine total number of new locations used, we sorted the UTM coordinates for each snake and counted the number of locations greater than six meters apart.

We analyzed directionality of movements between successive locations for the four treatment groups and that of individual snakes (to determine if individuals exhibited different patterns), using the Watson's U_n^2 -test for randomness (Batschelet 1981). Directionality was further analyzed by dividing data for individual snakes into movements between consecutive locations between six and 99 meters; and 100 meters and over. We determined the extra-experimental effects of year and sex by first separating data into separate seasons. If a significant departure from randomness was found for any group or individual snake during any component tested, movements between successive locations were tested for a mean direction (bearing) using the Rayleigh R-test (Batschelet 1981).

Condition

To assess changes in condition of the rattlesnakes we calculated growth rates for each snake by determining total change in snout-vent length (svl), and number of new rattle segments added over the course of the study. The relative importance of experimental and extra-experimental effects on the regression of the natural log-transformed body mass (logmass) to svl was determined using MANOVA tests (Neter et al. 1990). To compare the relative condition of the treatment groups during the study, we calculated residuals of the regression of logmass to svl. Changes in condition over the entire study were determined by averaging the change in mass for each snake during the periods before and after treatment.

RESULTS

From 1 June 1994 to 1 December 1996, 28 western diamondbacks (*Crotalus atrox*) and five black-tailed rattlesnakes (*C. molossus*) were captured opportunistically (Table 2). Of these, 19 adult western diamondbacks implanted with radio-transmitters were located a total of 1,648 times between August 1994 and December 1996. Mean number of locations per snake were 87 ± 49 , with a range of five to 187 total locations per individual. Fourteen rattlesnakes were involved in the relocation experiment, with seven as translocated animals (five males and two females); and seven as controls (four males and three females). The remaining five snakes (one male and four females) were lost before treatment and are

considered to be non-experimental animals.

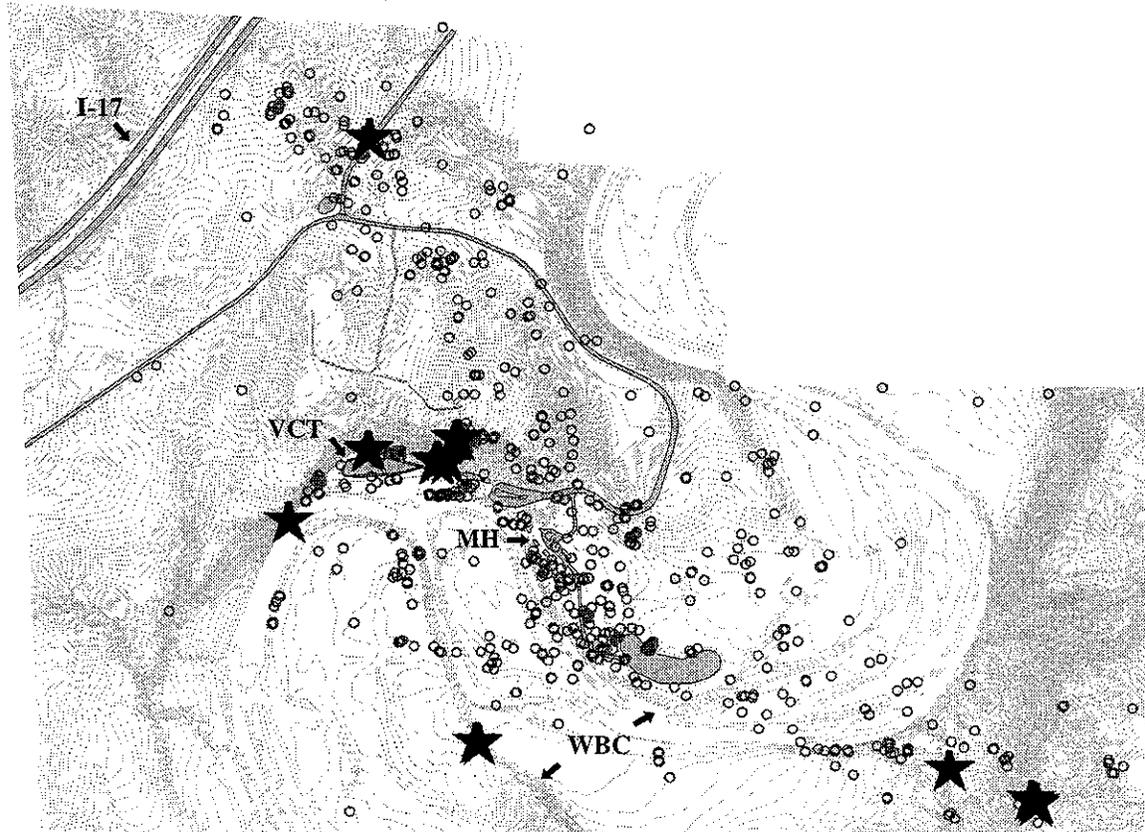
LOCATION OF HIBERNACULA AND FORAGING AREAS

The location of hibernacula and foraging areas were determined for 13 rattlesnakes on the monument. Nine snakes hibernated in five crevices or small caves in the limestone cliffs west of and directly behind the visitor center, while the remaining four hibernated in various sites throughout the monument, including crevices and caves, an abandoned root cellar, and a roadcut (Figure 3). Almost all sites, regardless of location, had a south- or east-

Table 2. Capture data for western diamondbacks (*Crotalus atrox*) and black-tailed rattlesnakes (*C. molossus*) at Montezuma Castle National Monument (Castle Section) between 1 June 1994 and 1 December 1996. For each snake, the date of capture, species, age, sex, measurements, number of segments on the rattle string, and receiver channel number, if implanted, are listed. Under "Age", "juv" represents juvenile (first or early second-year snakes), and "subad" represents sub-adult (late second or third-year) snakes. Under "Sex", a "U" indicates an unknown sex animal. "SVL" represents snout-vent length, measured in cm, and "Mass" is measured in grams. Missing data indicates that measurements were not taken.

| DATE | SPECIES | AGE | SEX | SVL (cm) | MASS (g) | # RATTLES | CHANNEL |
|----------|----------|-------|-----|----------|----------|------------|---------|
| 06/16/94 | atrox | adult | F | | | | |
| 07/09/94 | atrox | juv | F | ~20 | | 4 | |
| 07/09/94 | atrox | juv | F | ~17 | | 2 | |
| 07/20/94 | atrox | adult | M | 67 | 230 | | |
| 08/02/94 | atrox | adult | F | 101 | 520 | 14 | 19 |
| 08/12/94 | atrox | adult | F | 78.5 | 270 | | 24 |
| 08/23/94 | atrox | juv | U | | | 1 (button) | |
| 08/23/94 | atrox | adult | F | 75.5 | 268 | 8 | 27 |
| 08/28/94 | atrox | adult | M | 78 | 334 | 4 | 03 |
| 09/16/94 | molossus | adult | M | 99.5 | 662 | | 31 |
| 09/23/94 | atrox | adult | F | 89.5 | 604 | 9.5 | 36 |
| 10/03/94 | atrox | adult | M | 104 | 840 | 11 | 41 |
| 03/16/95 | atrox | adult | M | 100 | 827.7 | 6 | 35 |
| 05/01/95 | atrox | adult | M | 111 | 1038.9 | 9 | 47 |
| 06/21/95 | atrox | adult | M | 119.5 | 1225 | 10.5 | 25 |
| 07/03/95 | atrox | adult | F | 90 | 412.1 | 8 | 23 |
| 07/26/95 | atrox | adult | M | 139.7 | 1681.5 | 6.5 | 34 |
| 08/01/95 | atrox | adult | M | 121.5 | 1144 | 8.5 | 37 |
| 08/01/95 | molossus | subad | U | 62.5 | 211 | 5 | |
| 08/01/95 | molossus | subad | U | 64.5 | 246 | 2 (broken) | |
| 08/23/95 | atrox | adult | F | 77 | 484.6 | 11 | 39 |
| 08/25/95 | molossus | adult | M | | 763 | 11 | |
| 09/25/95 | atrox | adult | M | 85.10 | 426 | 10 | 40 |
| 10/12/95 | atrox | adult | M | 108.5 | 1583.3 | 9.5 | |
| 03/22/96 | atrox | adult | F | 100 | 554 | 8.5 | 43 |
| 03/25/96 | atrox | adult | M | 99 | 741 | 8.5 | 16 |
| 03/31/96 | atrox | juv | U | 38 | 39 | 2 | |
| 04/15/96 | atrox | adult | F | 102 | 483 | 10.5 | 22 |
| 05/01/96 | atrox | adult | F | 102 | 436 | 7.5 | 31 |
| 05/13/96 | molossus | subad | U | 74.5 | 193 | 4.5 | |
| 07/26/96 | atrox | adult | M | 98.8 | 526 | 9.5 | 29 |
| 10/27/96 | atrox | juv | M | 48 | | 4 | |
| 10/29/96 | atrox | adult | F | 86 | 445 | 7.5 | |

Rattlesnake Hibernation and Foraging Locations



○ Individual Rattlesnake Locations
During Active (Foraging) Period
(March - October)

★ Hibernation Sites

200 0 200 400 600 800 1000
METERS

N



Figure 3. Location of hibernacula and foraging locations for 19 adult western diamondbacks at Montezuma Castle National Monument, Arizona, between September 1994 and December 1996, showing snake locations, hibernacula, topography, roadways, streams, and manmade features (see Methods for study description). Open circles are one location of one snake (blotches represent multiple locations); stars are hibernation sites for single snakes or several individuals. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

facing exposure. Although the modal hibernaculum contained only one telemetered individual, one larger cave in the cliffs behind the visitor center was the joint hibernacula of five telemetered snakes.

One rattlesnake (Channel 41) spent several weeks at a hibernation site after beginning hibernation in 1994, and then moved to a new and final site (which was his preferred hibernation site in subsequent years); a second rattlesnake (Channel 22) repeated this pattern after initially entering hibernation in 1996. The average frequency of this hibernation site "switching" in the resident rattlesnakes was 0.10 during the study, but every resident snake studied over at least two hibernation periods ultimately returned to its same preferred hibernation site by December of every year. Complete emergence and dispersal from hibernacula occurred, on average, from mid-March to mid-April. Return to hibernacula and ingress usually occurred between early and mid-October, although in 1996 at least one male and one female were surface-active into November. At least one rattlesnake, Channel 36, followed nearly the same migratory paths during ingress and egress from her hibernation site in 1995, 1996, and 1997.

Non-relocated rattlesnakes did not disperse more than one kilometer in a straight-line distance from their hibernaculum during the summer foraging season. Foraging areas for snakes on the monument were located in riparian habitats, mesquite bosque, and upland vegetative communities dominated by creosotebush (*Larrea tridentata*), crucifixion-thorn (*Canotia holocantha*), and oak (*Quercus turbinella*) (see Figure 3). In general, individual rattlesnakes did not forage near hibernation sites in cliffs but dispersed away from these areas during the warm months.

Successful foraging events were documented primarily through anecdotal information, such as the presence of food bulges (boluses) in snakes' stomachs and guard hairs on the teeth of one rattlesnake, although one snake, Channel 41, was located while consuming a northern mockingbird (*Mimus polyglottos*). Five non-relocated snakes were observed to have obvious bulges in their stomachs. Based on the average size of these boluses, and on the location of many snakes in woodrat (*Neotoma sp.*) middens during the active season, it is likely that woodrats were a common prey item. Two rattlesnakes were also located with very large (approx-

mately 15 centimeters [cm] x 10 cm x 5 cm) bulges in their bodies, so it is likely that adult cottontail rabbits (*Sylvilagus sp.*) were also taken.

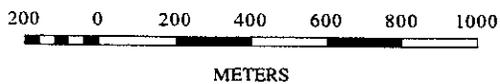
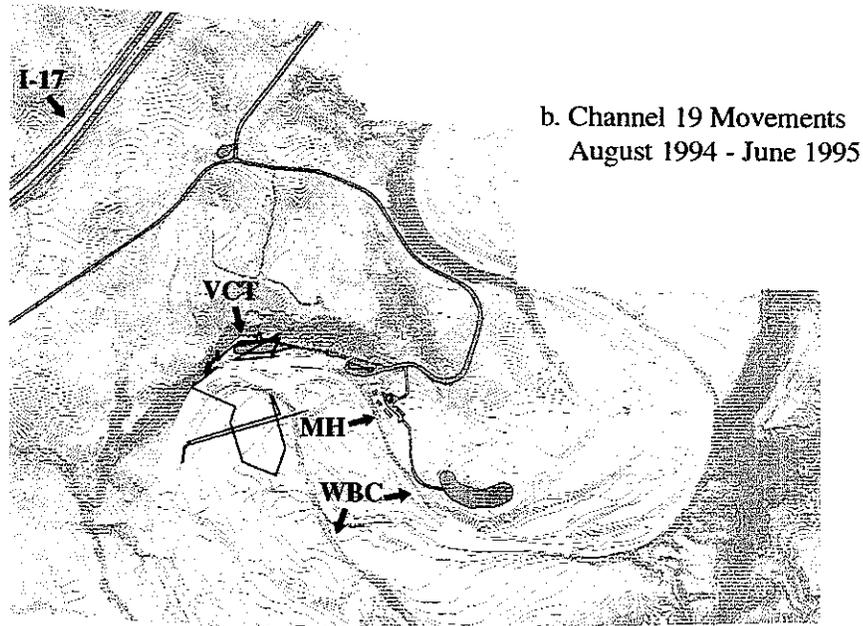
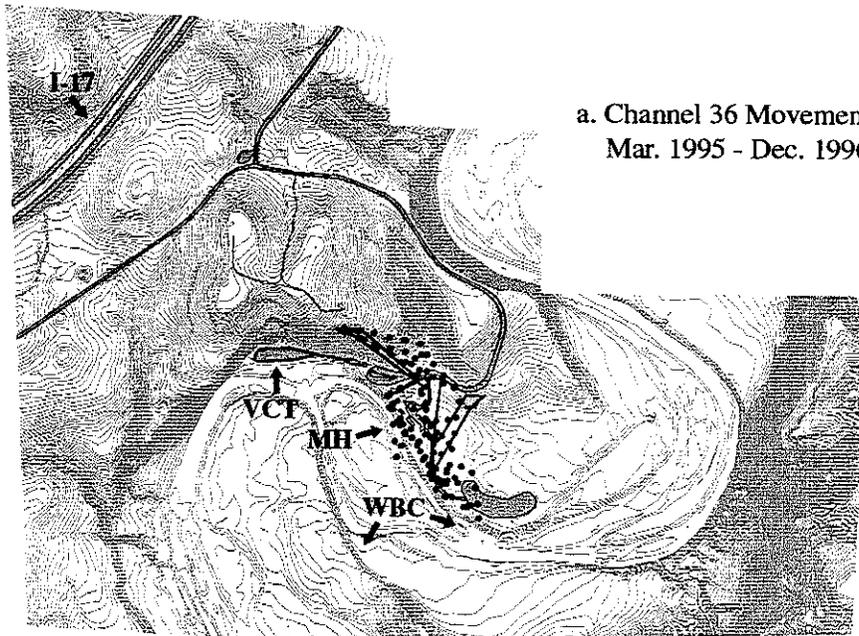
REASONS FOR RATTLESNAKE PRESENCE IN HUMAN USE AREAS

One potential reason for rattlesnake presence in visitor and housing areas, particularly during the spring and fall months, would be the proximity of these areas to potential hibernacula. During migrations to and from hibernacula, at least three rattlesnakes usually traveled through the visitor use and/or housing areas. Seven of nine rattlesnakes that had hibernacula in the cliffs behind the visitor center did not travel through the visitor use area, but either used a culvert and small canyon north of the visitor area to access the cliffs from the east, or accessed hibernacula from the west (the top of the cliffs). Channel 36 (a female) is an example of a snake that used this strategy (Figure 4a) and Channel 19 (also a female) is an example of a snake that traveled directly through the visitor area during migrations to and from her hibernation site (Figure 4b).

Another reason for rattlesnake presence in human use areas may be foraging opportunities for snakes around the visitor access and housing areas during the summer months. Although the concentration of rodents, birds, lizards, and/or rabbits in these areas compared to other areas of the monument was not documented, 12 of 19 rattlesnakes were located in either visitor access or housing areas at least once during their active period, and seven of these snakes had frequencies of location in these areas greater than 0.25 (Table 3). Some documented examples of foraging around human use areas include: Channel 41, observed foraging for several days at an open compost pit, and consuming a mockingbird behind the housing area; Channel 03, foraging for nearly a week in a woodrat nest in an abandoned utility cart; and Channel 25, observed near the visitor trail with a rabbit-sized stomach bulge. In spite of a relatively high frequency of locations by researchers of rattlesnakes in human use areas, the snakes were almost never seen by park staff or visitors: discounting the original capture of snakes in these areas, the total number of subsequent sightings of

Table 3. Frequency of locations of rattlesnakes in visitor use and housing areas at Montezuma Castle during the summer active period, August 1994 to October 1996. "V.C." refers to visitor use areas; "Housing" is the park staff housing area; "# of Snakes" is the total number of individuals using each area (some individuals used both areas); "Minimum Frequency" is the lowest frequency of use in an area by any individual; "Maximum Frequency" is the highest use frequency by any individual; and "Average Frequency" is the average frequency of locations for the snakes observed in each area.

| LOCATION | # OF SNAKES | MINIMUM FREQUENCY | MAXIMUM FREQUENCY | AVERAGE FREQUENCY |
|------------------|-------------|-------------------|-------------------|-------------------|
| V.C. and Housing | 12 | 0.02 | 0.97 | 0.33 |
| V.C. | 11 | 0.07 | 0.76 | 0.31 |
| Housing | 8 | 0.01 | 0.21 | 0.07 |



-  Movements Between Successive Locations, Aug. 1994 - 1995
-  Movements Between Successive Locations, Aug. 1995 - Dec. 1996



Figure 4a. and b. Movement pattern between successive locations for two female western diamondback rattlesnakes, from March 1995 to December 1996 at Montezuma Castle National Monument, Arizona (see Methods for experiment description). a. Channel 36, b. Channel 19. Solid lines connect successive locations between August 1994 and August 1995; dotted lines connect successive locations between August 1995 and December 1996. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

telemetered rattlesnakes in these areas was less than 10. In several cases, rattlesnakes were located less than five meters from the visitor trails, within view of hundreds of people walking by that day, and yet were not seen until pointed out by researchers. In the one case where a snake (Channel 19) was seen several times in one day, she had been captured and placed on the opposite side of the trail from her intended direction of travel.

EFFECTS OF RELOCATION

One relocated rattlesnake, Channel 23, disappeared two days after the relocation experiment in 1995, and was not located again during the study despite repeated efforts to find her, including the use of aerial tracking. This snake is thus excluded from the relocated group after treatment in the following results.

No obvious initial effects of relocation could be determined by observing rattlesnakes immediately after relocation in 1995. The vegetation was too thick to permit observers to move far enough away so that they were not likely to be impacting the animals' behavior: both groups of rattlesnakes immediately took cover under the nearest shelter, where they remained until after dark. One relocated rattlesnake, Channel 41, climbed approximately one and a half meters into a crucifixion-thorn shrub and remained there. This was the only observation of a western diamondback climbing into vegetation during the study.

Changes in Hibernacula and Foraging Area Use After Treatment

The three animals relocated in 1995 did not return to the monument that year, but found hibernacula in cliffs in the relocation area. In 1996, two of these rattlesnakes returned to the monument: Channel 41 returned to his original pre-relocation hibernation site, and Channel 34 probably also returned to his original hibernation site (based on overlapping activity ranges in 1995 and 1996). Channel 25 returned to the same hibernation site in the relocation area that he had used after treatment in 1995.² None of the three rattlesnakes relocated in 1996 returned to the monument

that year. During the 1997 hibernation period, Channel 16 (relocated in 1996) returned to his original hibernation site on the monument. Location of final hibernacula for the control snakes did not change after the experiment, and the location and use of hibernation sites for relocated animals differed more in physical location than in qualitative type.

Egress from and ingress to initial hibernacula for the relocated rattlesnakes occurred during the same time periods as that of control and resident rattlesnakes. Two of three rattlesnakes relocated in 1995 spent several weeks at an initial hibernation site after beginning hibernation, then moved to different and final sites; two of four remaining relocated snakes and one control switched hibernacula in 1996. The average frequency of this hibernation site "switching" was significantly higher in relocated rattlesnakes than in the controls in 1995, but not in 1996 (Table 4).

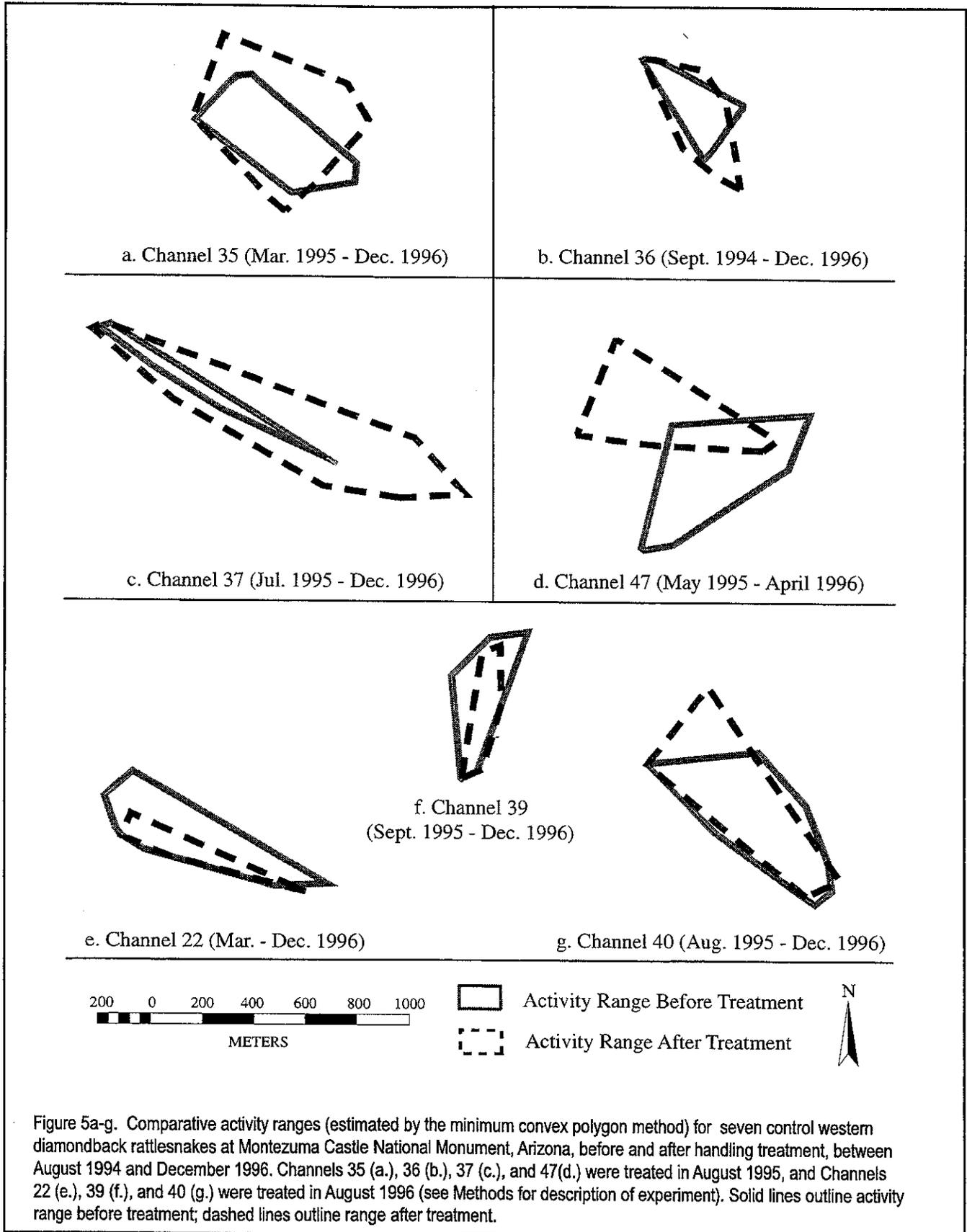
Foraging areas for control snakes did not change before and after treatment. Foraging areas for relocated snakes immediately after relocation were in upland vegetative communities dominated by crucifixion-thorn (*Canotia holocantha*), mariola (*Parthenium incanum*), threeawn (*Aristida sp.*), creosotebush (*Larrea sp.*), and juniper (*Juniperus sp.*) Three rattlesnakes were located several times in mesquite (*Prosopis sp.*) bosque within a few weeks after relocation. Channel 25 remained in the relocation area, and spent most of the summer of 1996 foraging in riparian habitat (this snake was also located exclusively in the riparian area at the monument prior to his relocation). Channels 41 and 34 returned to the monument in 1996, and were located within the same habitats and several times under the same retreat sites (i.e., boulders, burrows, and woodrat middens) that they had used prior to their relocation.

Change in the incidence of successful foraging was difficult to ascertain, due to snakes being tracked at different time intervals and to the paucity of direct foraging observations and obvious boluses in snakes' bodies. At least one snake, Channel 34, was observed with three separate food bulges in his body after relocation.

² Two additional new western diamondbacks were found outside the relocation hibernaculum of Channel 25 in the spring of 1996, and one male western diamondback was found outside the relocation hibernaculum of Channel 16 in the spring of 1997.

Table 4. Frequency of rattlesnakes moving to new hibernation sites after entering hibernation at Montezuma Castle National Monument during 1995 and 1996. "Treatment Group" refers to control or relocated snakes, "N" is the total number of snakes in each group each year. "Year" is the year of the study beginning the hibernation period. "Frequency of Switching" is the number of snakes in each group that moved to a new hibernation site after initially entering hibernation, divided by the number of snakes in the group. "P²" and "p-Value" are the Pearson's Chi-squared test statistic and the probability value for that statistic, and * denotes significance at the p < 0.05 level.

| TREATMENT GROUP | N | YEAR | FREQUENCY OF SWITCHING | P ² | p-VALUE |
|-----------------|---|------|------------------------|----------------|---------|
| control | 6 | 1995 | 0.00 | 5.14 | 0.02* |
| relocated | 3 | 1995 | 0.67 | | |
| control | 6 | 1996 | 0.17 | 1.5 | 0.22 |
| relocated | 6 | 1996 | 0.50 | | |



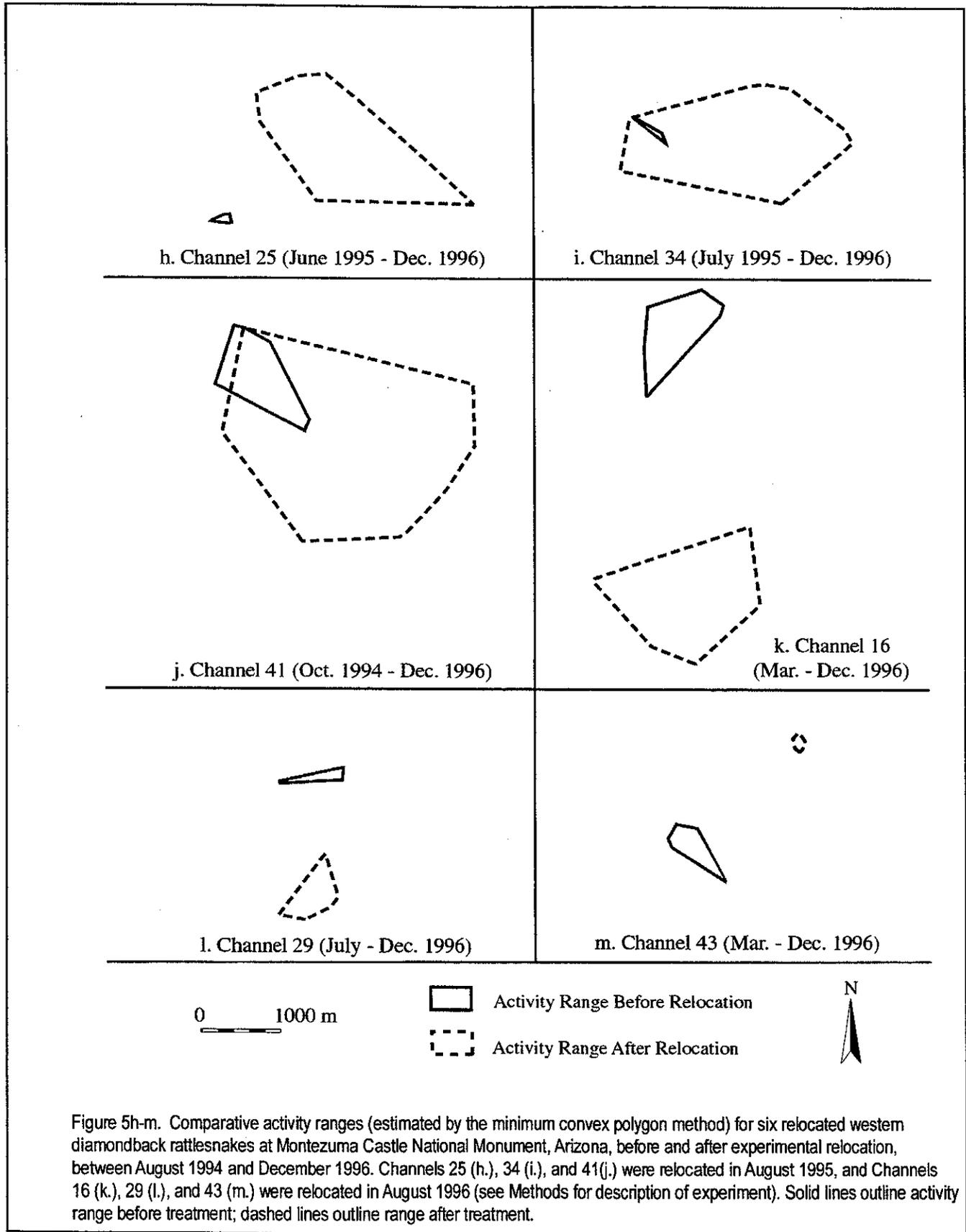


Figure 5h-m. Comparative activity ranges (estimated by the minimum convex polygon method) for six relocated western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, before and after experimental relocation, between August 1994 and December 1996. Channels 25 (h.), 34 (i.), and 41(j.) were relocated in August 1995, and Channels 16 (k.), 29 (l.), and 43 (m.) were relocated in August 1996 (see Methods for description of experiment). Solid lines outline activity range before treatment; dashed lines outline range after treatment.

Changes in Activity Range Size

Comparative activity ranges for each rattlesnake before and after treatment are illustrated on pages 13-14 in Figures 5a-n; controls in Figures 5a-g; and relocated snakes in Figures 5h-n. Maps of each snake's locations and activity range in relation to study site features are given in Appendix A.

The activity range sizes for control rattlesnakes before handling treatment did not differ significantly from their sizes after handling (during equivalent time periods) ($t = 0.02$; $d.f. = 6$; $p = 0.98$) (Figure 6). The average range size for the control group was 8.76 ± 6.82 ha before treatment, and 8.95 ± 6.41 ha after treatment.

The average range size for the relocated group was 24.27 ± 22.16 ha before relocation, and 59.58 ± 57.22 ha after relocation (during equivalent time periods). Four of six relocated rattlesnakes had activity range sizes that increased greatly after treatment, and two had activity ranges that decreased when compared to that before relocation (Figure 7, page 16). Thus, although there was a trend for the average activity range of the relocated group to increase after relocation, due to individual variation, this was not statistically significant ($t = -1.15$; $d.f. = 5$; $p = 0.30$).

When the two relocated and control groups were compared (excluding snakes with less than 10 weeks of data), the average activity range size of the control rattlesnakes did not differ from that of the relocated snakes before the experiment ($t = -0.44$; $d.f. = 8$; $p = 0.67$). While there was a trend for the relocated snakes to have larger activity ranges than controls after relocation, this was not significant ($t = -1.56$; $d.f. = 8$; $p = 0.16$) (Figure 8, page 16).

There were no significant extra-experimental impacts on the average activity range size of non-relocated rattlesnakes at Montezuma Castle National Monument. There was no impact of study year on the ranges ($t = -1.82$; $d.f. = 19$; $p = 0.09$): in 1995, the average range size was 11.91 ± 14.12 ha; and in 1996, it was 17.41 ± 11.61 ha. Although there was a trend for males to have large activity ranges, there was no statistically significant impact of sex on the average activity range size ($t = 0.62$; $d.f. = 13$; $p = 0.55$). The average activity range size for males was 19.03 ± 16.01 ha, and for females 8.48 ± 3.87 ha. The variation in range size was significantly higher for males than for females ($F = 13.45$; $p = 0.002$).

Changes in Movement Patterns

Average distance moved per day

The average distance moved per day was determined for each snake by dividing the distance moved between successive locations (only those within four days of each other) by number of days elapsed. When we compared the data during the active season between study years, we found that the average number of days between successive locations was significantly greater in 1996 (2.99 ± 0.83 days) than in 1995 (2.35 ± 0.92 days) ($t = -8.11$; $d.f. = 480$; $p = 0.00$). This discrepancy might have resulted in extra-experimental impacts: for two controls, the average distance moved per day was significantly greater in 1995 than in 1996 ($F = 6.57$; $d.f. = 1$; $p = 0.02$ and $F = 5.77$; $d.f. = 1$; $p = 0.02$, respectively). Thus, we analyzed these data separately for each year.

In 1995, there was no significant difference in average

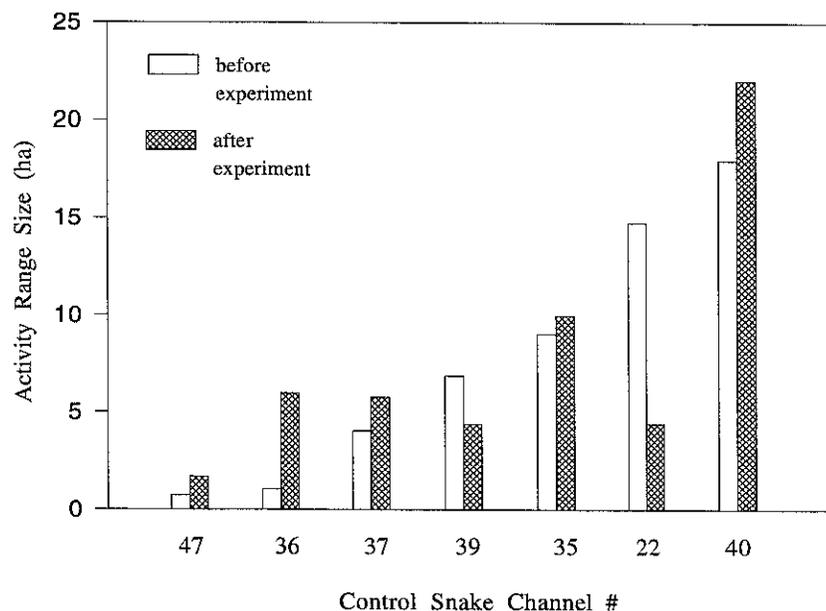


Figure 6. Comparative activity range sizes (estimated in hectares by the minimum convex polygon method for seven control western diamond-back rattlesnakes before and after handling treatment. Treatment occurred during a relocation experiment at Montezuma Castle National Monument, Arizona, conducted between August 1994 and December 1996 (see Methods for description of experiment). Channel numbers 47 through 40 identify individual rattlesnakes.

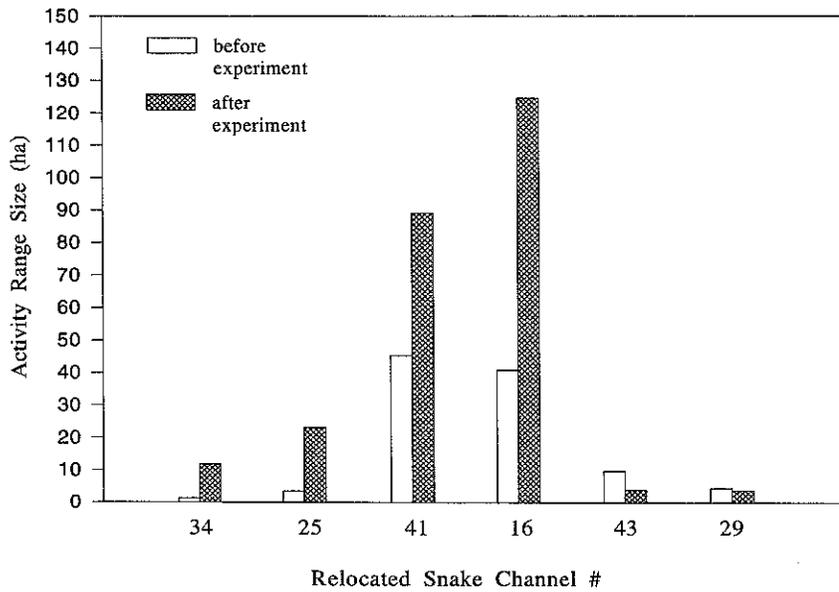


Figure 7. Comparative activity range sizes (estimated in hectares by the minimum convex polygon method) for six relocated western diamondback rattlesnakes before and after relocation, between August 1994 and December 1996. Experimental relocation occurred at two kilometers from the visitor center of Montezuma Castle National Monument, Arizona (see Methods for description). Channels 34 through 29 identify individuals.

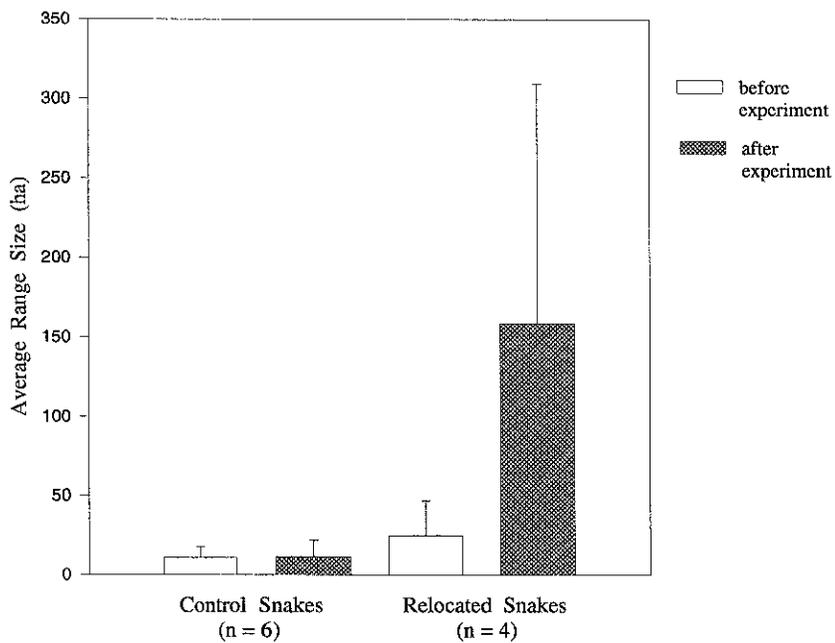


Figure 8. Average activity range sizes (estimated in hectares by the minimum convex polygon method) for six control compared to four relocated western diamondback rattlesnakes before and after a relocation experiment at Montezuma Castle National Monument, Arizona, between August 1994 and December 1996. Control rattlesnakes were given handling treatment; relocated snakes were relocated at two kilometers from the monument visitor center (see Methods for description of experiment).

distance moved per day during the active season for the control snakes before and after the experiment ($t = -0.79$; $d.f. = 3$; $p = 0.49$), but there was a significant difference for relocated snakes before and after the experiment ($t = 7.76$; $d.f. = 2$; $p = 0.02$) (Figure 9). The average distance moved per day by the control snakes before treatment was 28.21 ± 59.59 meters per day (m/day) and 32.50 ± 42.78 day after. For relocated snakes, the average movement before relocation was 28.58 ± 41.21 m/day and 108.33 ± 115.48 m/day after. When between-group comparisons were made, the control and relocated snakes did not differ significantly in distance moved per day before the experiment ($t = -0.84$; $d.f. = 129$; $p = 0.40$), but did differ significantly after the experiment ($t = -3.27$; $d.f. = 72$; $p = 0.002$).

In 1996, the movement patterns were not as clear. There was no significant difference in average distance moved per day for the control snakes before and after the experiment ($t = 2.86$; $d.f. = 2$; $p = 0.10$), and there was also no significant difference for relocated snakes before and after treatment ($t = -0.26$; $d.f. = 2$; $p = 0.82$) (Figure 10, page 18). The average distance moved per day by the control snakes before treatment was 25.41 ± 37.45 m/day and 35.34 ± 55.28 m/day after the experiment. For relocated snakes, the average movement per day was 45.06 ± 52.18 m/day before relocation and 41.09 ± 87.55 m/day after.

When between-group comparisons were made for the 1996 data, control and relocated snakes did not differ significantly in average distance moved per day before ($t = -1.82$; $d.f. = 78$; $p = 0.07$), nor after the experiment ($t = 0.33$; $d.f. = 29$; $p = 0.74$). This

result is likely due to small sample size (only three snakes in each group) and to individual variation among the relocated animals. One of the relocated rattlesnakes, Channel 43, a non-gravid female, moved less than 300 meters from her release site in 1996 until she went into hibernation.

The distance moved per day by the control snakes the first few months after treatment did not differ significantly from the second year after treatment ($t = 0.67$; $d.f. = 2$; $p = 0.57$), but the relocated snakes moved significantly farther the first few months after relocation when compared with the second year ($t = 6.31$; $d.f. = 2$; $p = 0.02$) (Figure 11, page 18). When control and relocated snakes were compared during the second year after treatment, there was no significant difference in average distance moved per day ($t = -1.24$; $d.f. = 119$; $p = 0.22$). Control snakes moved an average of 27.92 ± 47.52 meters per day the second year after the experiment, and relocated snakes averaged 31.26 ± 33.96 m/day.

When we compared the daily movements during the hibernation period between study years, we found that there was no significant difference in the number of days between successive locations: there were 11.68 ± 12.72 days between locations in 1995 and 8.993 ± 7.28 days in 1996 ($t = 0.83$; $d.f. = 197$; $p = 0.41$). Consequently, the data were combined. The control and relocated groups were tested for differences only during the winters immediately preceding and following the experiment. There was no significant difference in the average distance moved per day for hibernating control snakes before and after the experiment ($t = -1.36$; $d.f. = 117$; $p = 0.18$): the distance per day was 0.62 ± 0.71 m/day before the

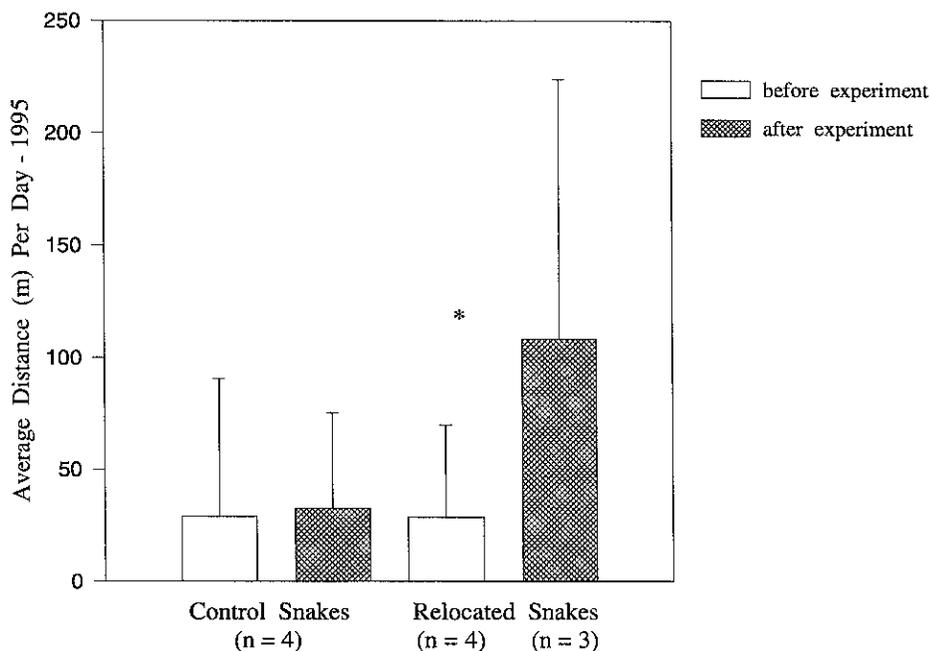


Figure 9. Average distance (in meters) moved per day during the 1995 active season for control and relocated western diamondback rattlesnakes before and after a relocation experiment at Montezuma Castle National Monument, Arizona, between March 1995 and November 1995 (see Methods for description of experiment) ($t = 7.76$; $d.f. = 2$; $p = 0.02$). * indicates significance at the $p < 0.05$ level.

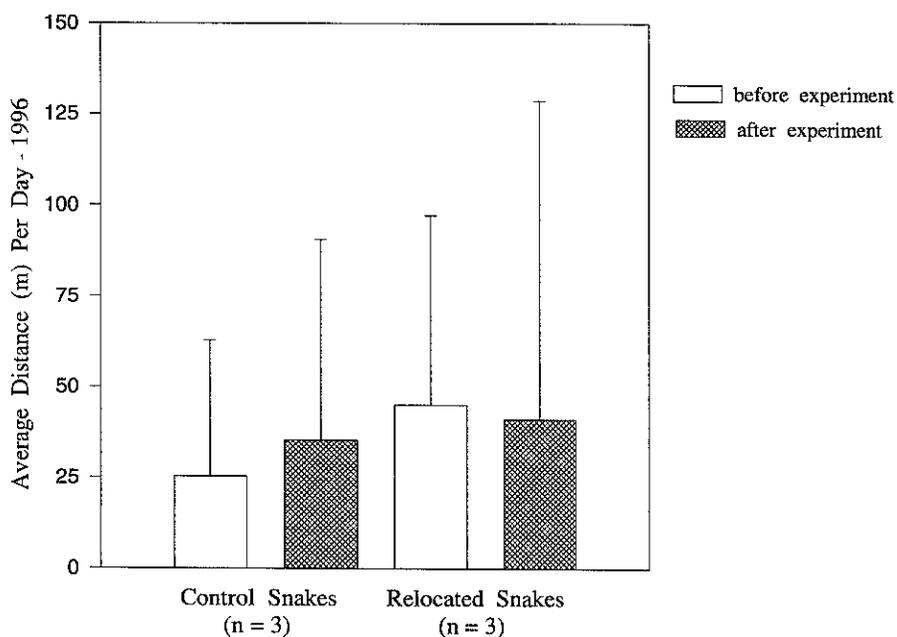


Figure 10. Average distance (in meters) moved per day during the 1996 active season for control and relocated western diamondback rattlesnakes before and after a relocation experiment at Montezuma Castle National Monument, Arizona, between March 1996 and November 1996 (see Methods for description of experiment).

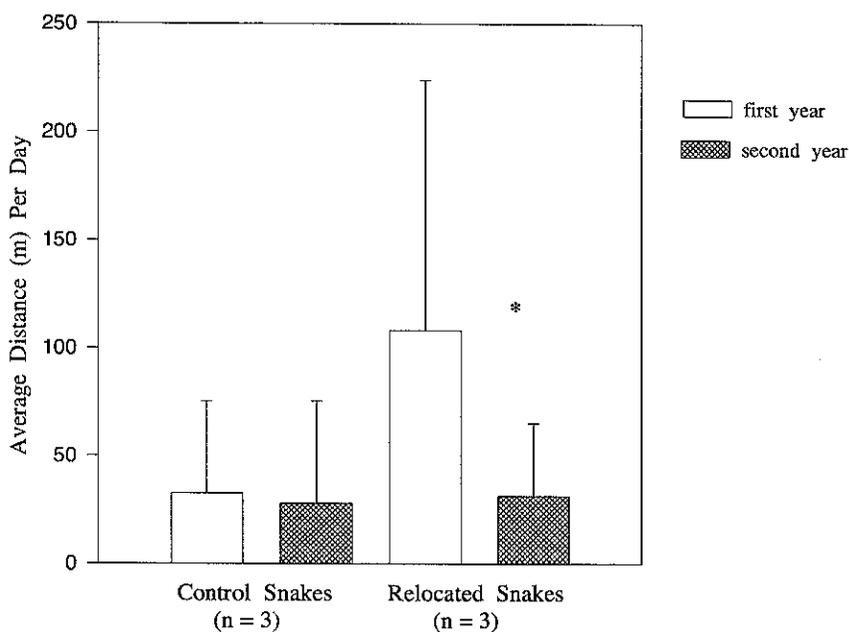


Figure 11. Distance moved per day (in meters) after treatment by control and relocated western diamondback rattlesnakes the first few months after treatment (August - November 1995) compared to the second year after treatment (March - November 1996) ($t = 6.31$; $d.f. = 2$; $p = 0.02$). Handling treatment or relocation occurred during a relocation experiment at Montezuma Castle National Monument, Arizona (see Methods for description of experiment). * indicates significance at the $p < 0.05$ level.

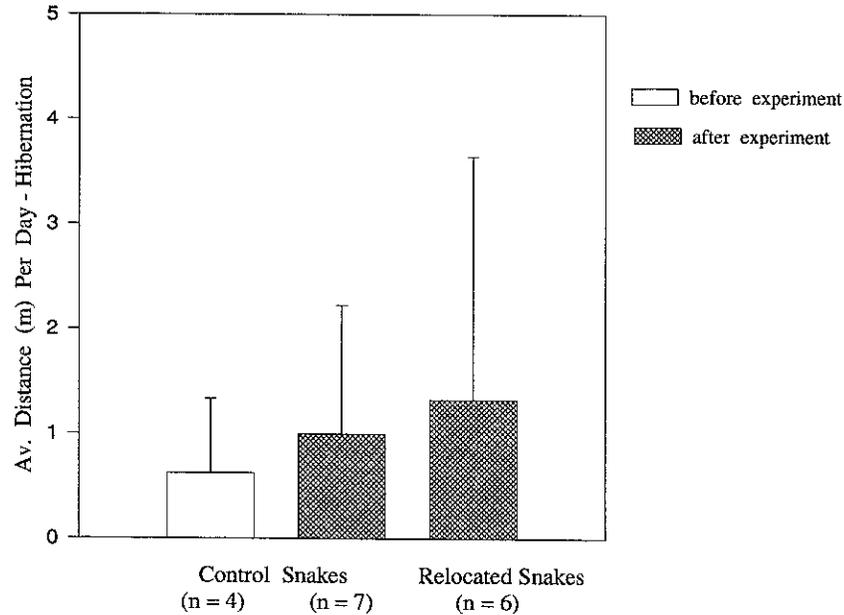


Figure 12. Average distance moved per day (in meters) during hibernation (October - March) before and after a relocation experiment for control western diamondback rattlesnakes, and for relocated and control rattlesnakes after the experiment at Montezuma Castle National Monument, Arizona, in 1995 and 1996 (see Methods for description).

experiment and 1.00 ± 1.23 m/day after. There was also no significant difference between hibernating control and relocated snakes after treatment ($t = .39$; d.f. = 63; $p = 0.70$), but there was a trend for relocated snakes to move a greater distance (1.48 ± 2.44 m/day) (Figure 12).

Other than year of the study, there was no effect of extra-experimental factors on the average distance moved per day during the active season (extra-experimental factors were not deemed pertinent for hibernating snakes). When compared among spring, dry summer, wet summer, and fall seasons, there was no significant difference in either 1995 ($F = 1.41$; d.f. = 3; $p = 0.26$), or 1996 ($F = 0.186$; d.f. = 43; $p = 0.91$). When the average distance moved per day during the active season was compared between males and fe-

males, there was no significant difference in 1995 ($t = 1.66$; d.f. = 208; $p = 0.10$) nor in 1996 ($t = 0.58$; d.f. = 163; $p = 0.56$). In both years, there was a trend for males to move a greater distance per day than females.

Frequency of movement

The frequency of movement did not differ between control and relocated groups before or after the experiment ($\chi^2 = 50.50$; d.f. = 51; $p = 0.49$) (Table 5). Within groups, the frequency did not differ significantly before and after the experiment for controls ($Z = -1.48$; $p = 0.14$) or relocated snakes ($Z = -0.53$; $p = 0.59$). The frequency of movement for controls was 0.67 ± 0.26 before and 0.79 ± 0.14 after treatment, and for relocated snakes was 0.71 ± 0.20

Table 5. Frequency of movement for control and relocated rattlesnakes before and after treatment during relocation experiment at Montezuma Castle National Monument, August 1994 - October 1996. "Group (Status)" lists each treatment group and its status; "# Movements" is the number of movements between successive locations; "Total # Sampled" is the total number of locations collected; and "p-Value" is the test statistic for each group compared before and after treatment.

| GROUP (STATUS) | # MOVEMENTS | TOTAL # SAMPLED | FREQUENCY OF MOVEMENT | p-VALUE |
|--------------------|-------------|-----------------|-----------------------|---------|
| control (before) | 83 | 142 | .58 | 0.14 |
| control (after) | 100 | 129 | .78 | |
| relocated (before) | 62 | 85 | .73 | 0.59 |
| relocated (after) | 78 | 94 | .83 | |

before and 0.82 ± 0.06 after.

Neither year nor season of study significantly impacted the frequency of movement of non-relocated snakes. In 1995, these snakes had a frequency of movement of 0.66 ± 0.26 , and in 1996, the frequency of movement was 0.805 ± 0.15 ($\chi^2 = 30.61$; d.f. = 34; $p = 0.63$). The frequency of movement did not differ among the four seasons ($\chi^2 = 81.94$; d.f. = 72; $p = 0.20$).

Sex of the non-relocated snakes also did not significantly impact the frequency of movement ($\chi^2 = 16.61$; d.f. = 19; $p = 0.62$). Males had a combined frequency of movement of 0.71 ± 0.20 compared to 0.67 ± 0.21 for females.

Number of new locations used

The frequency of new locations used (total number of locations used by an individual snake divided by the actual number of new locations used) also did not differ significantly between the groups before or after the experiment ($\chi^2 = 56.68$; d.f. = 60; $p = 0.60$) (Table 6). The frequency of new location use for control snakes was significantly greater before the experiment when compared to after at the $p \leq 0.05$ level ($Z = -1.99$; $p = 0.05$). Controls had a frequency of 0.62 ± 0.82 new locations used before the experiment, and 0.82 ± 0.64 after treatment. This frequency was not significantly different for relocated snakes before and after the experiment ($Z = -1.21$; $p = 0.22$): they used a frequency of 0.76 ± 0.16 new locations before and 0.86 ± 0.16 after treatment. At least one relocated snake, Channel 41, returned to the same area several times in the first few months after relocation. Relocated rattlesnakes that returned to the monument had slightly decreased frequencies of new site use: they were reusing the same sites that they had used before relocation.

Neither year nor season had significant impacts on the frequency of new locations used by non-relocated rattlesnakes. The frequency of new locations used by year was 0.71 ± 0.20 in 1995 and 0.86 ± 0.09 in 1996 ($\chi^2 = 77.93$; d.f. = 75; $p = 0.39$). The frequency of new locations was not different among the four seasons ($\chi^2 = 78.09$; d.f. = 93; $p = 0.87$).

Sex of the non-relocated snakes did not have a significant effect on the frequency of new site use ($\chi^2 = 24.89$; d.f. = 25; $p = 0.47$). Males had a frequency of 0.78 ± 0.16 new locations used, compared to 0.71 ± 0.15 for females.

Total distance traveled from experimental site to hibernation

The total distance moved between the experimental release site and the first hibernation site used after the experiment were compared between years for non-relocated snakes. No statistically significant difference was found between years, although there was a trend of a shorter average distance moved after the experiment in 1996 (1059.76 ± 400.00 meters) when compared to 1995 (2231.89 ± 1127.82 meters) ($t = 1.98$; d.f. = 5; $p = 0.10$). Thus, the movements of all snakes were combined for both years in this analysis.

There was no significant difference in the distance moved between experiment release site and hibernation site of control and relocated snakes: control snakes moved an average of 1729.55 ± 1040.13 meters between release site and first hibernation site, and relocated snakes moved an average of 3677.74 ± 2488.45 meters ($t = -1.61$; d.f. = 11; $p = 0.14$) (Figure 13). There was a trend for most relocated snakes to move relatively farther.

When the total distance moved during 1996 by snakes subjected to the experiment in the previous year was examined, there was a trend for the relocated group to move farther than the controls, but this was not statistically significant at the $p \leq 0.05$ level ($t = -2.60$; d.f. = 4; $p = 0.06$). For perspective, the total distance moved by Channel 41 between release in 1995 to final hibernation site in 1996 was 15.7 kilometers (km) (13.09 km before returning to his original activity range), and Channel 34 moved 14.5 km during the same time period (9.4 km before returning to his original activity range). For comparison, during the same time period, the only similar-sized control male (Channel 37) moved 9.1 km.

Males moved an average of 2256.61 ± 1098.52 meters and females an average of 1026.79 ± 372.95 meters. There was no significant difference in total distance moved after treatment to hibernation between males and females, although males tended to move farther than females ($t = 1.82$; d.f. = 5; $p = 0.13$).

Directionality of consecutive movements

When the movements between consecutive locations for each treatment group were analyzed for departure from random, those of the control snakes did not differ significantly from random before ($U_n^2 = 0.12$; $p > 0.05$) nor after treatment ($U_n^2 = 0.15$; $p > 0.05$) (Figure 14 a. and b).

Table 6. Frequency of new locations used by control and relocated rattlesnakes before and after treatment during relocation experiment at Montezuma Castle National Monument, August 1994 - October 1996. "Group (Status)" lists each treatment group before and after treatment; "# New Locations" is number of new locations used by each treatment group during that time period; "Total # Sampled" is the total number of locations collected for each group; "Frequency of Location Use" is the frequency of new locations used by each; and "p-Value" is the test statistic for each group compared before and after treatment. * indicates significance at the $p < 0.05$ level.

| GROUP (STATUS) | # NEW LOCATIONS | TOTAL # SAMPLED | FREQUENCY OF LOCATION USE | p-VALUE |
|--------------------|-----------------|-----------------|---------------------------|---------|
| control (before) | 147 | 219 | .67 | 0.05* |
| control (after) | 176 | 220 | .78 | |
| relocated (before) | 100 | 136 | .74 | 0.22 |
| relocated (after) | 167 | 196 | .85 | |

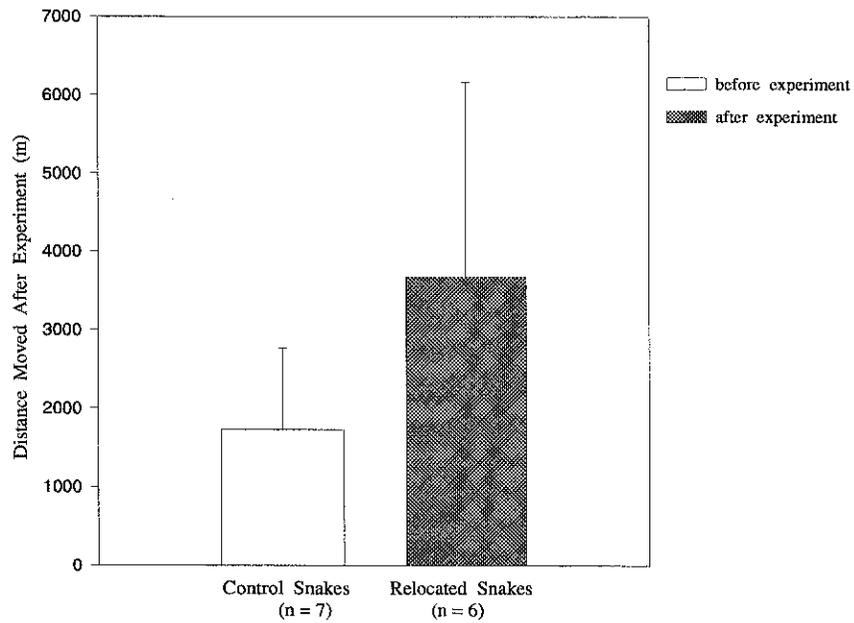


Figure 13. Average distance moved (in meters) from experimental release site to first hibernation site for control and relocated western diamondback rattlesnakes during experimental relocation study at Montezuma Castle National Monument, Arizona. Movement occurred between August and November, during 1995 and 1996 (data for both years is combined; see text for description of experiment).

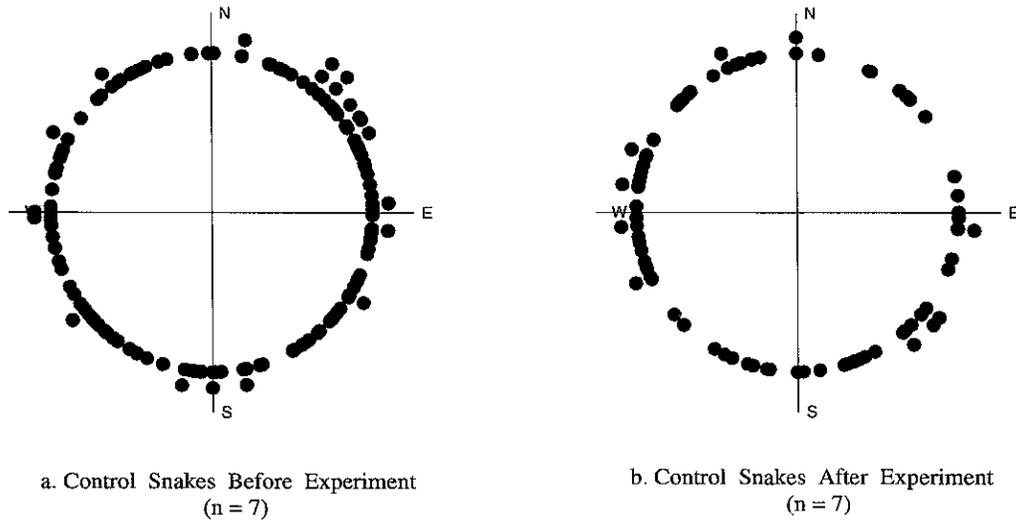
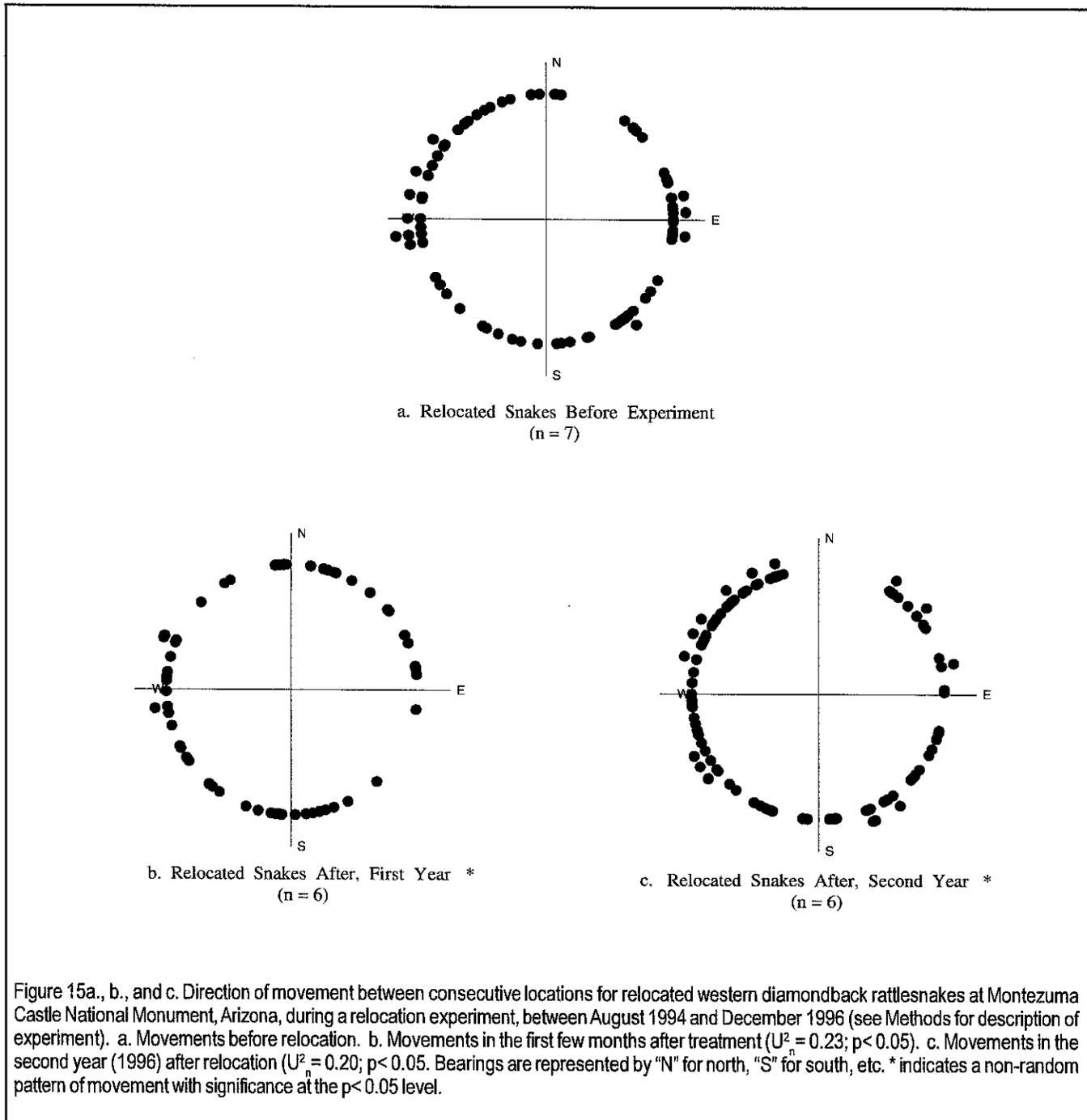


Figure 14a. and b. Direction of movement between consecutive locations for control western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, during a relocation experiment between August 1994 and December 1996 (see Methods for description of experiment). a. Movements before handling treatment. b. Movements after treatment. Bearings are represented by "N" for north, "S" for south, etc.

The directional movement pattern between consecutive locations for the relocated snakes did not depart significantly from random ($U_n^2 = 0.07$; $p > 0.05$) before treatment, but was significantly non-random both in the first few months after relocation ($U_n^2 = 0.23$; $p < 0.05$) and the second year after relocation ($U_n^2 = 0.20$; $p < 0.05$) (Figure 15 a., b., and c.). However, this non-random pattern did not translate into a significant mean bearing either immediately following relocation ($R = 9.91$; $p > 0.05$) or the year after ($R = 16.57$; $p > 0.05$).

Only three individual snakes had consecutive movements that departed significantly from random before or after treatment. Channel 29, a relocated male, showed non-random movements in the first few months after relocation ($U_n^2 = 0.20$; $R = 5.34$; significant mean bearing of 235° ; $p < 0.05$); Channel 34, also a relocated male, the second year after relocation ($U_n^2 = 0.21$; $R = 10.83$; significant mean bearing of 237° ; $p < 0.05$); and Channel 39, a control female, in the first few months after treatment ($U_n^2 = 0.19$; $R = 4.16$; significant mean bearing of 210° ; $p < 0.05$).



We expected that long-distance movements would tend to be directional dispersal events whereas short-distance movements would be random within foraging patches; however, when the movements between consecutive locations were divided into less than 100 meters and greater than 100 meters and analyzed separately there was no clear pattern. Two individuals exhibited non-random movement patterns: Channel 37, a control male, in his movements over 100 meters before treatment ($U_n^2 = 0.23$; not enough data to determine the significance of the mean bearing);

and Channel 34, in his movements between 6 and 99 meters the second year after relocation ($U_n^2 = 0.24$; $R = 7.96$; significant mean bearing of 224° ; $p < 0.05$).

When the data were analyzed by season for non-relocated rattlesnakes, only during dry summer was there significant departure from random with a significant mean bearing of 110° ($U_n^2 = 0.18$; $R = 19.56$; $p < 0.05$) (Figure 16 a, b, c, and d).

There was no clear pattern of directional movements when seasonal effects were examined for individual non-relocated

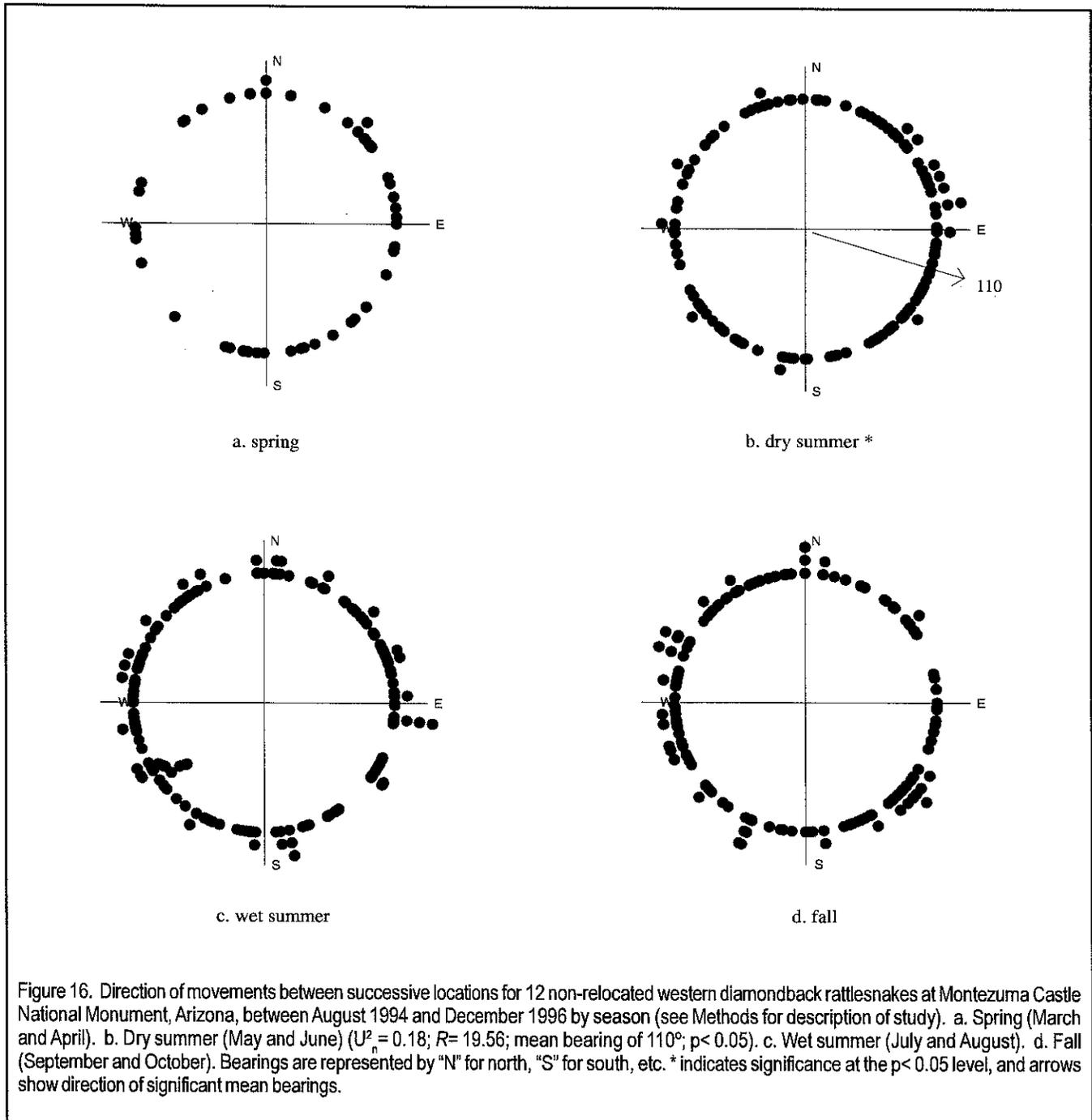


Table 7. Movements of individual snakes between successive locations with significant departures from random during the spring, dry summer, wet summer, and fall seasons at Montezuma Castle National Monument, August 1994 - October 1996. "CHANNEL" refers to channel number of the snake, "SEASON" refers to the period in which the movements were significant, "YEAR" refers to the year of the study, and "MEAN BEARING" gives the significant mean bearing, if found, or other information if no significance was found.

| CHANNEL | SEASON | YEAR | U^2_n | R | MEAN BEARING |
|---------|------------|------|---------|------|------------------------------|
| 43 | spring | 1996 | 0.22 | - | not enough data to determine |
| 16 | dry summer | 1996 | 0.19 | 6.40 | 71 |
| 34 | dry summer | 1996 | 0.20 | 4.34 | not significant |
| 41 | dry summer | 1996 | 0.18 | 5.52 | not significant |
| 41 | wet summer | 1995 | 0.21 | 7.12 | 147 |
| 25 | wet summer | 1996 | 0.22 | 4.35 | not significant |
| 34 | wet summer | 1996 | 0.25 | 6.18 | 177 |
| 35 | fall | 1995 | 0.22 | 5.03 | not significant |
| 29 | fall | 1996 | 0.24 | 5.34 | 244 |
| 37 | fall | 1996 | 0.33 | 7.04 | 121 |

snakes (Table 7).

Extra-experimental effects of year and sex were analyzed within each season to reduce extraneous variability as much as possible. When the data were analyzed by year of the study, only in 1996 during dry summer was there a significant non-random movement pattern ($U^2_n = 0.20$; $p < 0.05$), without a significant mean bearing ($R = 15.00$; $p > 0.05$). When the data for each season were analyzed by sex, only the males during dry summer had consecutive movements that departed significantly from random, with a significant mean bearing of 47° ($U^2_n = 0.20$; $R = 11.34$; $p < 0.05$).

Changes in Condition

We weighed and measured two rattlesnakes in the field (unanesthetized) and in the veterinarian's office (anesthetized) less than two weeks apart. In these duplicate measurements, the field measurements of snout-vent length were slightly shorter (between one and three percent) than the office measurements. We did not manipulate the data to correct for the discrepancy between office and field measurements because the difference between the two methods was less than five percent.

As expected, mass and snout-vent length (svl) were strongly correlated in this population of western diamondbacks ($R^2 = 0.87$; $p = 0.0002$) when all measurements were combined (Figure 17a). Most snakes grew very little during the study: non-relocated snakes grew an average of 2.09 ± 3.09 cm in length and added an average of 0.90 ± 0.91 new segments to their rattle string every 12 months. Because of this limited growth, and also because svl measurements tended to be slightly inaccurate, changes in svl alone were not used as an indicator of condition.

Treatment did not have an effect on the relationship of mass to svl in this population ($F = 0.184$; $d.f. = 3$; $p = 0.91$), and interaction between the different status levels was not significant

($F = 1.28$; $d.f. = 3$; $p = 0.31$) (Figure 17b).

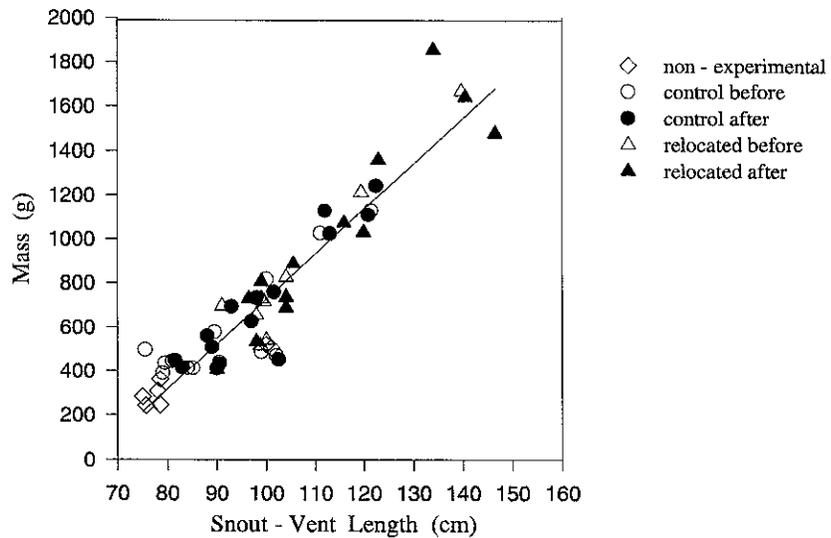
Changes in the mass of at least four individual snakes over the course of study showed a cyclical pattern roughly corresponding to season (Figure 18, page 26), but there were insufficient data to determine if this effect was significant.

Extra-experimental impacts on the relationship between mass and svl were also examined. When analyzed separately from other variables, year of the study did not contribute significantly to the relationship model ($F = 1.65$; $d.f. = 1$; $p = 0.21$). However, there was a significant effect of sex of the snake on the relationship between mass and svl ($F = 10.83$; $d.f. = 1$; $p = 0.002$): males were significantly longer and heavier than females, as expected for rattlesnakes (Figure 19, page 26).

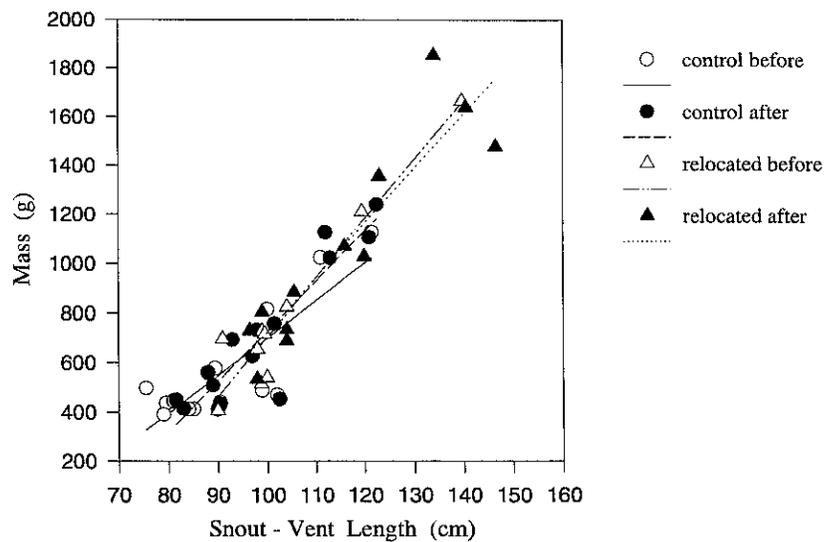
When comparative health indices of the snakes (residuals of the natural log of snake mass to svl) were compared between control and relocated snakes, there was no significant difference between the groups before treatment ($t = 0.07$; $d.f. = 21$; $p = 0.95$) or after treatment ($t = 0.18$; $d.f. = 25$; $p = 0.86$) (Figure 20, page 27).

When extra-experimental effects were examined, these residual indices did not differ between years of the study ($t = 1.69$; $d.f. = 37$; $p = 0.10$). Residuals were significantly different between males and females ($t = 3.27$; $d.f. = 35$; $p = 0.002$); males had a slightly positive average residual while females had a slightly negative residual and significantly larger variation among individuals ($F = 8.03$; $p = 0.007$) (see Figure 19).

There was no significant difference when the average change in mass was compared within the control group before and after the experiment, ($t = 0.60$; $d.f. = 5$; $p = 0.58$) and also no significant difference for relocated snakes before and after treatment ($t = 0.05$; $d.f. = 3$; $p = 0.96$). When comparisons were made between groups, there was no significant difference in average change in mass before the relocation experiment ($t = -0.43$; $d.f. = 8$; $p = 0.68$)



a. All Snakes Combined



b. Treatment Groups

Figure 17a. and b. Mass and snout-vent length (svl) for 19 western diamondbacks, each measured three times a year, at Montezuma Castle National Monument, Arizona, between August 1994 and October 1996 (see Methods). a. All individuals, with common regression line ($R^2=0.87$; $p=0.0002$). b. Experimental individuals (7 control and 6 relocated snakes), with each group having a separate regression line. * indicates significance at $p<0.05$.

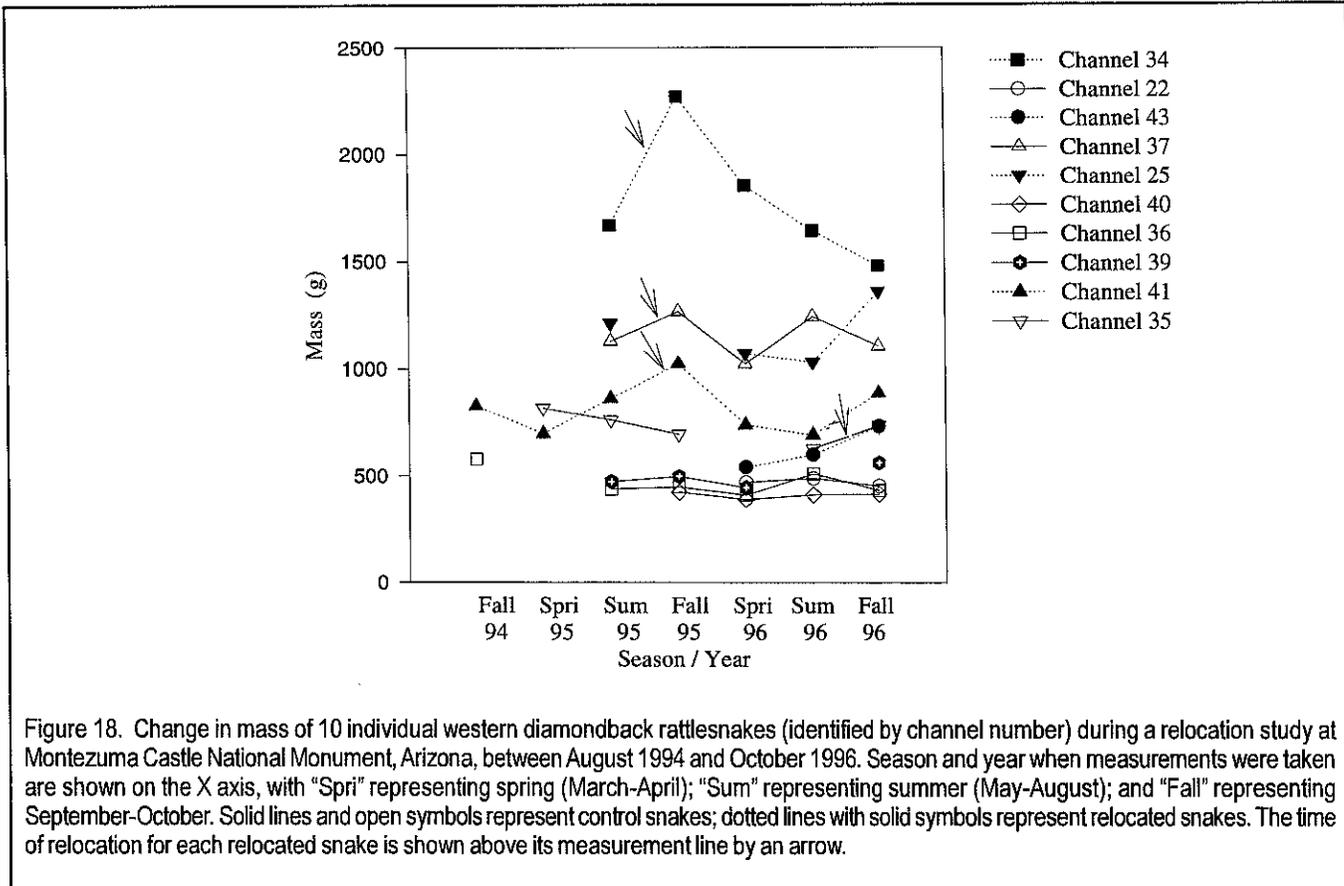


Figure 18. Change in mass of 10 individual western diamondback rattlesnakes (identified by channel number) during a relocation study at Montezuma Castle National Monument, Arizona, between August 1994 and October 1996. Season and year when measurements were taken are shown on the X axis, with "Spri" representing spring (March-April); "Sum" representing summer (May-August); and "Fall" representing September-October. Solid lines and open symbols represent control snakes; dotted lines with solid symbols represent relocated snakes. The time of relocation for each relocated snake is shown above its measurement line by an arrow.

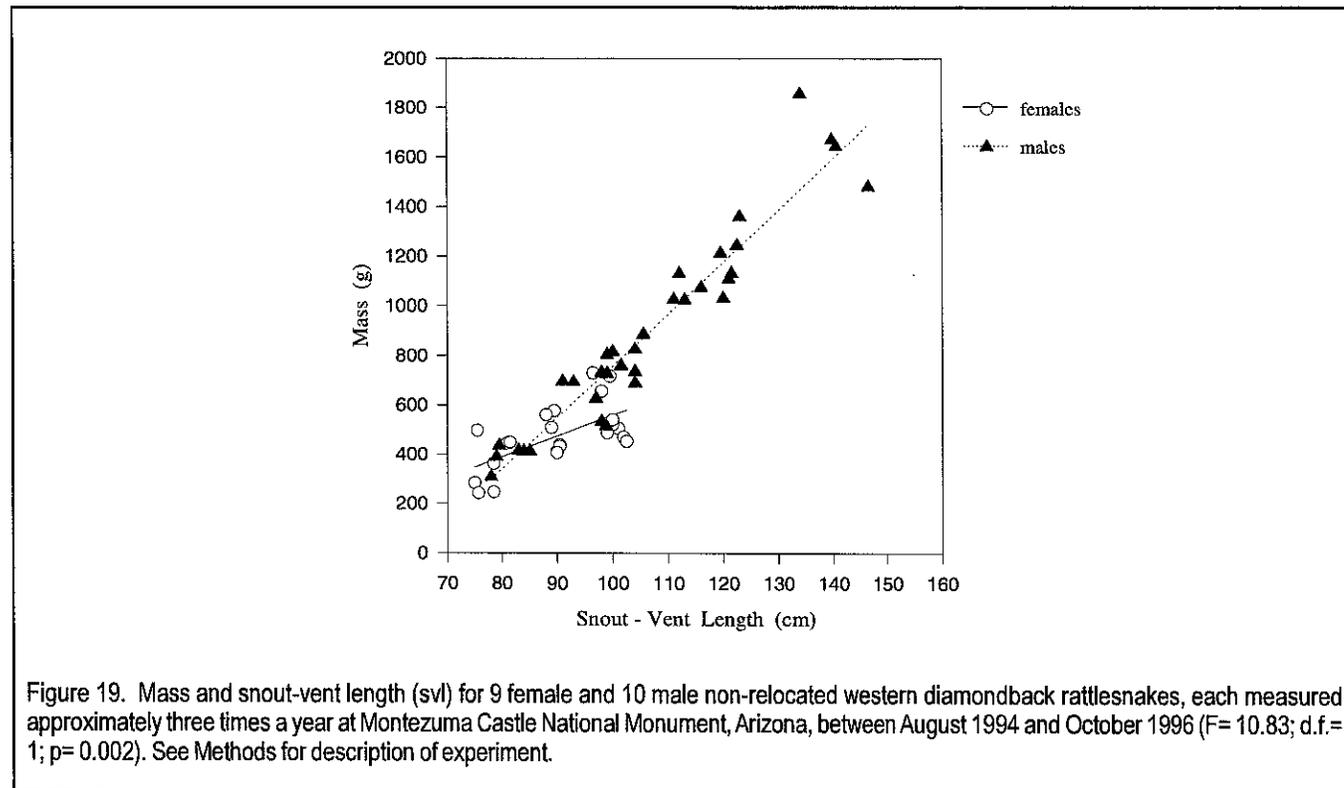


Figure 19. Mass and snout-vent length (svl) for 9 female and 10 male non-relocated western diamondback rattlesnakes, each measured approximately three times a year at Montezuma Castle National Monument, Arizona, between August 1994 and October 1996 ($F= 10.83$; $d.f.= 1$; $p= 0.002$). See Methods for description of experiment.

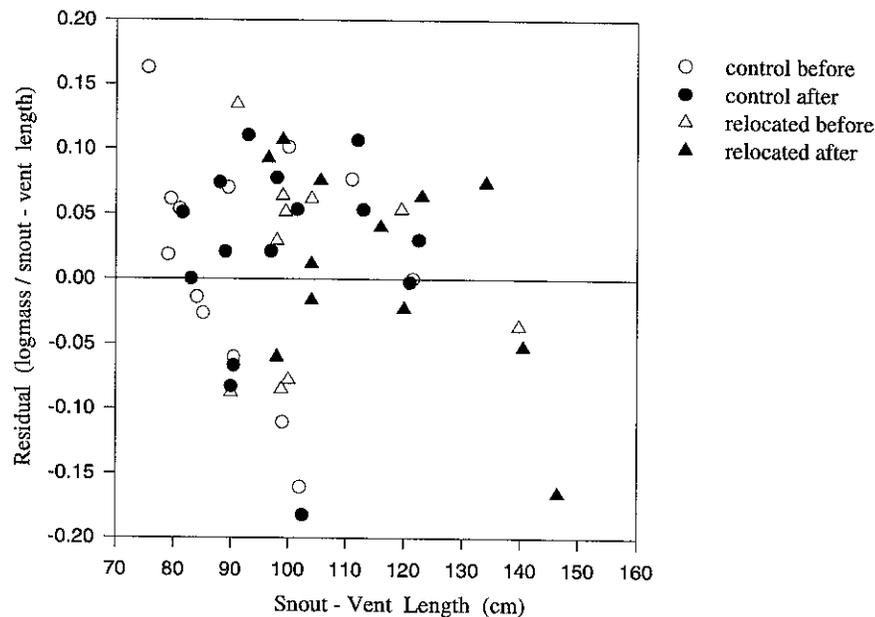


Figure 20. Residuals of the regression of the log of mass ("logmass," in grams) to snout-vent length ("svl," in centimeters), versus svl for 7 control and 6 relocated western diamondback rattlesnakes before and after treatment during a relocation experiment at Montezuma Castle National Monument, Arizona, between August 1994 and October 1996. Each snake was measured approximately three times a year (see Methods for description of experiment). The expected normal regression line is drawn through the Y-axis.

or after ($t = 0.65$; $d.f. = 9$; $p = 0.53$). When the average change in mass was compared between males and females, there was no significant difference ($t = 0.08$; $d.f. = 14$; $p = 0.93$), nor was there a significant difference between years ($t = -0.77$; $d.f. = 14$; $p = 0.45$).

Mortality

Two confirmed mortalities occurred during the study, and both were relocated animals. The first, a male (Channel 34) returned to the monument in the spring of 1996. This snake steadily lost weight from the fall of 1995 until the time of his death in January 1997 (see Figure 19). He was found dead outside his hibernaculum several days to a week after death, and probably succumbed to disease or exposure. There were no obvious signs of predation, but his mouth was filled with bloody, viscous fluid, suggesting that a bacterial or viral infection was present at the time of death. The second mortality was Channel 43, a female, that did not return to the monument after relocation. Parts of her body and whole transmitter were found in the relocation area in the fall of 1997, but her time and mode of death were not clear, as she was last located alive three months prior to this. She was found less than 50 meters from a recently-bulldozed site, but it was not evident whether this was involved in her death.

One relocated female (Channel 23) disappeared after relocation, and a non-experimental female (Channel 24) also disappeared before treatment (it was last located next to a roadway).

Mortality can neither be ruled out nor confirmed in either of these cases.

Bare transmitters were found for three snakes, Channels 31, 37, and 41, during the study, suggesting either that the transmitters were spontaneously expelled from the body (for example, through a wound in the skin and/or body wall), or that mortality occurred. The transmitter of Channel 31, a female, was found less than two weeks after implantation away from human use areas on the monument, without obvious signs of trauma. In 1997, the transmitter of Channel 37, a male, was found near the visitor trail in front of the Castle ruins, next to his rattle. His transmitter contained obvious bite marks and natural predation is likely in this case. Also in 1997, the transmitter of Channel 41 was found in an area of residential homes approximately one kilometer northeast of the monument, with one puncture which was likely made by a canine tooth or large beak. The snake had never been seen in this area while alive, and the last location while alive was about 100 meters west of the monument's visitor center.

Homing Abilities After Relocation

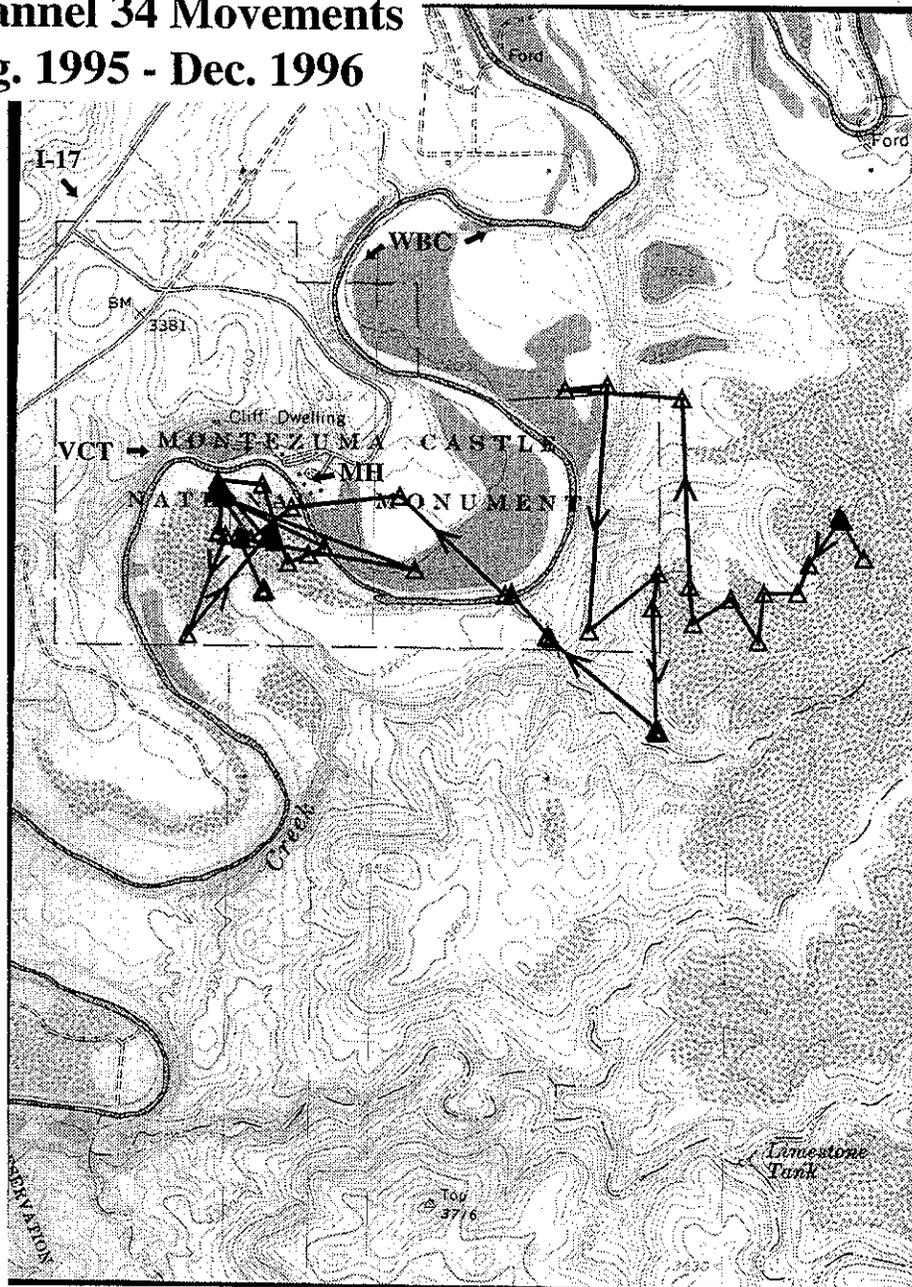
As previously noted, two of four rattlesnakes relocated in 1995 returned to the monument in 1996. Channel 34 returned to his original activity range on the monument in early spring of 1996, several weeks after emerging from hibernation. Over about a five-day period, he appeared to travel directly from his hiberna-

tion site through a large wash to the monument, a distance of approximately 1 kilometer (Figure 21a). He was located within 50 meters of his last location before treatment within a week of returning to the monument. Channel 41 did not immediately return to the monument after relocation, but was back on the monument by June 1996 and within his original activity range by July 1996. He, too, appeared to take a straight and direct path to the monument from the relocation area (Figure 21b, page 30). He was located several times under the same boulders and woodrat

middens that he had used during his active periods in 1994 and 1995 prior to relocation.

Two of three rattlesnakes relocated in 1996 returned to the monument in 1997. Locations were not collected regularly for rattlesnakes in 1997, so the exact route followed by Channels 16 and 29 on their return to the monument, and their respective dates of arrival, are not known. Channel 29 was found within his original activity range in early July 1997, and Channel 16 was found on a trail near the visitor center by park rangers in late July 1997.

Channel 34 Movements Aug. 1995 - Dec. 1996



200 0 200 400 600 800 1000
METERS



Movements Between Successive Locations

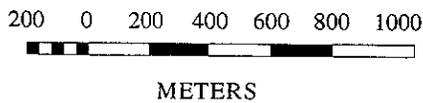
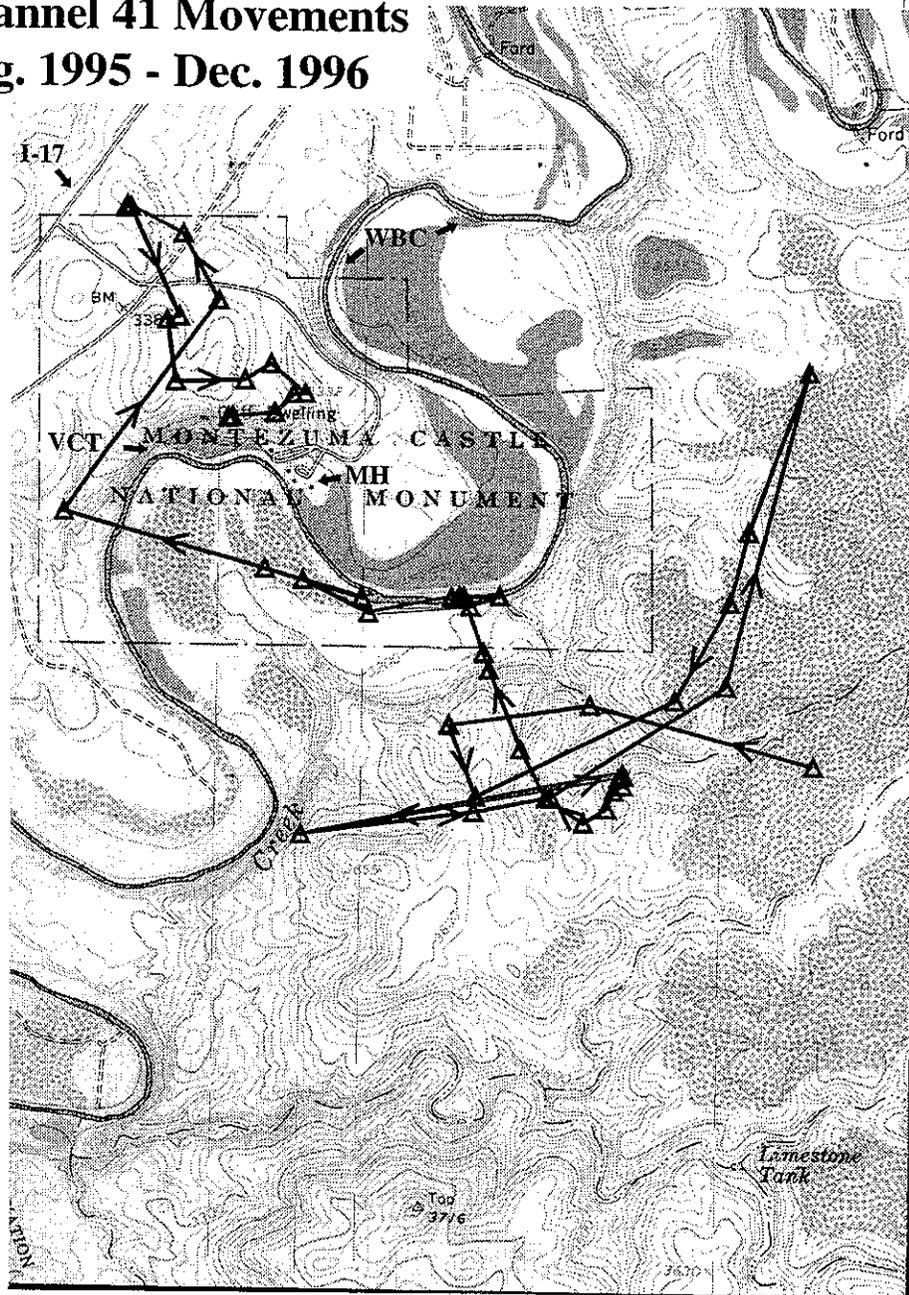


One Location of Snake



Figure 21a. Movement pattern between successive locations for Channel 34, male relocated western diamondback rattlesnake, from experimental relocation at two km from Montezuma Castle National Monument, Arizona, on August 1995, to December 1996 (see Methods for experiment description). Open triangles represent one location of the snake, lines connect successive locations, and arrows indicate direction of travel. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

Channel 41 Movements Aug. 1995 - Dec. 1996



Movements Between Successive Locations



One Location of Snake



Figure 21b. Movement pattern between successive locations for Channel 41, male relocated western diamondback rattlesnake, from experimental relocation at two km from Montezuma Castle National Monument, Arizona, on August 1995, to December 1996 (see Methods for experiment description). Open triangles represent one location of the snake, lines connect successive locations, and arrows indicate direction of travel. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

DISCUSSION

LOCATION OF HIBERNACULA AND FORAGING AREAS

The most striking discovery about the location of hibernacula and foraging areas for non-relocated rattlesnakes at Montezuma Castle National Monument is the use constancy of these areas year after year. Although there was a low incidence of site "switching" during the hibernation period, the ultimate locations of individual snakes' hibernacula were exactly the same for all rattlesnakes studied over two or three hibernation seasons. This hibernation site fidelity has been observed in colubrid snake species (reviewed by Gregory 1984), in vipers such as *Vipera berus* (Viitanen 1967), and in rattlesnakes such as western diamondbacks (Beaupre 1995), eastern diamondbacks (*Crotalus adamanteus*) (Means 1977), great basin rattlesnakes (*C. viridis lutosus*) (Woodbury 1951), timber rattlesnakes (*C. horridus*) (Brown 1993), and various other species (Sexton et al. 1992). The location of these sites in large rock outcrops with south to southeast exposures is also typical of rattlesnakes (reviewed by Sexton et al. 1992).

The rattlesnakes in this study exhibited fidelity to general foraging areas as well as specific foraging sites (i.e., a specific woodrat midden). These types of site fidelity have also been found for western diamondbacks by Beaupre (1995), for timber rattlesnakes by Sealy (1997), and for other snakes, including European adders (*Vipera berus*) (Viitanen 1967), rat snakes (*Elaphe obsoleta*) (Weatherhead and Robertson 1990), and racers (*Coluber constrictor*) (Brown and Parker 1976). Foraging areas seemed to be determined on the basis of individual preference: some rattlesnakes foraged exclusively in riparian habitats, others exclusively in upland habitats, and still others were found in both habitat types during the course of an active season. The hypothesis that snakes learn preferred foraging regions or habitats while young and then return to these favored sites or to similar habitats throughout their adult lives has been suggested for rattlesnakes by H. Reinert (pers. comm.), and site fidelity to nesting areas has been demonstrated in pine snakes (Burger and Zappalorti 1991).

In general, rattlesnakes do not have large foraging or activity ranges, usually not dispersing more than four kilometers in a straight line from their hibernacula during the foraging season (King and Duvall 1990, Gannon and Secoy 1985). We found that western diamondbacks at Montezuma Castle had activity ranges averaging 30 hectares. This was larger than the average of 5.4 hectares noted for western diamondbacks in southern Arizona by Beck (1995), the only other study to date that has reported activity range sizes for this species. Published reports of average activity range size (calculated by the minimum convex polygon method) in other rattlesnake species tracked for at least a year include: 3.5 ha for tiger rattlesnakes (*Crotalus tigris*) and for black-tailed rattlesnakes in southern Arizona (Beck 1995), 21 ha for sidewinder (*C. cerastes*) in the eastern Mojave Desert of California (Secor 1994), 25 ha for massasaugas (*Sistrurus catenatus*) in Ontario, Canada (Weatherhead and Prior 1992), and 27 ha for timber rattlesnakes in New Jersey (Reinert and Zappalorti 1988b). As noted for many snake species

in a review by Macartney et al. (1988), most male western diamondbacks at Montezuma Castle had larger activity ranges than females, although there was also a high amount of variability among individuals.

Because the diet and incidence of successful foraging events for this population of rattlesnakes was not precisely determined, the implications that can be drawn about foraging ecology are limited. Based on anecdotal evidence from foraging locations in woodrat middens, and on the size of food boluses in the snake's stomachs, we presume that rodents make up the bulk of this population's diet, particularly woodrats. The diets of other western diamondback populations are also known to contain primarily small mammals, particularly woodrats (D. Duvall, pers. comm.), and also cottontail rabbits, ground squirrels (*Spermophilus sp.*), pocket gophers, pocket mice (*Perognathus sp.*), *Peromyscus sp.*, grasshopper mice (*Onychomys sp.*), and shrews, birds, lizards, insects, and carrion (Beavers 1976, Klauber 1972), all of which occur at Montezuma Castle (Ellison 1995). The inclusion of cottontail rabbits in this population's diet may be a result of maintenance of non-native lawns and frequent mowing of roadside vegetation, which appear to positively influence both the distribution and abundance of these prey items (pers. obs).

RATTLESNAKE PRESENCE IN HUMAN USE AREAS

An obvious reason for rattlesnake presence in visitor use and housing areas at Montezuma Castle National Monument is the proximity of these areas to suitable hibernacula: over half of the rattlesnakes tracked at the monument were hibernating in dens less than 100 meters from the main visitor trail. This phenomenon has also been documented at other national park areas. A study at Natural Bridges National Monument found that rattlesnakes sighted near the visitor center and/or staff housing areas were primarily migrating through these areas from hibernacula near the visitor center, on their way to summer foraging sites (Graham 1991, 1994).

Another reason for the presence of rattlesnakes around human use areas, particularly during the summer active periods, may be foraging opportunities for snakes. Artificially increased prey abundance and the presence of artificial refuges (i.e., under buildings) are cited as potentially important influences of rattlesnake distribution at the Arizona Sonoran Desert Museum in southern Arizona by Perry-Richardson and Ivanyi (1992). Graham (1994) demonstrated that there was an increased abundance of potential prey (rodents, lizards, and birds) around the visitor use and housing areas at Natural Bridges National Monument compared to other areas of the monument, and that several rattlesnakes were repeatedly located within or near these human use areas during the foraging season. He suggested that the increased abundance of prey in visitor use and housing areas might be due to the presence of non-native vegetation, which generally produces more biomass and seeds than native species, to garbage left by visitors or put out by staff, to bird feeding and watering, and/or to the presence of

refuge areas in the form of wood, lumber, or brush piles, thick vegetation, or loose soil for burrowing.

Anecdotal evidence from distribution of snake ranges, proportion of time spent in human use areas, and incidental observations of successful foraging events at Montezuma Castle support the hypothesis that foraging opportunities for rattlesnakes are high around human use areas. In addition, these areas are located within floodplain habitat, and a study of the comparative distribution and abundance of small mammals at the monument in 1993 and 1994 demonstrated that small mammals were more abundant in floodplain areas than in the surrounding uplands (Ellison 1995). It is not known, however, whether the prey concentration around human use areas at Montezuma Castle is actually denser than in outlying areas. To determine a causal relationship between the abundance of prey and presence of snakes in human use areas, more information is needed on the relative distribution of prey populations around the monument, and on the diet of this population of rattlesnakes.

Snakes that travel through or inhabit the visitor use areas may be habituated to the presence of large numbers of humans. However, although some rattlesnakes traveled directly through human use areas during spring and fall migrations, others seemed to follow circuitous paths to avoid these areas. Avoidance behaviors may be triggered by the presence of over 900,000 people a year at the visitor center, and/or by an earlier capture by park staff (see also Sealy 1997). Learned avoidance behavior is likely in rattlesnakes given that humans are potential predators (Duvall et al. 1985, Klauber 1972). Sealy (1997) suggests that rattlesnakes translocated short distances are likely to avoid previous capture sites in the future, and the low number of resightings of telemetered rattlesnakes after initial capture in visitor areas adds anecdotal support to this hypothesis, although the issue was not examined specifically in this study. Physical or temporal avoidance of areas regularly visited by humans has also been noted for timber rattlesnakes (Brown 1993), and suggested for rattlesnakes at Natural Bridges National Monument (Graham 1994).

We found that individual rattlesnake detectability was not high for Montezuma Castle staff or visitors. This implies that under most circumstances rattlesnakes at Montezuma Castle are not disposed toward revealing their presence by rattling or moving, even if approached closely. This observation is supported by other studies of free-ranging rattlesnakes, and it is thought that rattlesnakes use procrystis as the primary mechanism to avoid detection by predators (including humans) (May et al. 1996, Reinert and Zappalorti 1988b, Duvall et al. 1985, Klauber 1972, and C. Parent, pers. comm.). As well, rattlesnakes at Montezuma Castle did not strike at staff or researchers unless handled (see also Dart et al. 1992, Hardy 1986).

EFFECTS OF RELOCATION

There did not appear to be any impact of treating the control rattlesnakes with handling on subsequent movement patterns, behavior, or condition, and this result is consistent with other studies of telemetered free-ranging rattlesnakes (summarized in

Reinert 1992).

Changes in Hibernacula and Foraging Area Use After Relocation

All relocated rattlesnakes were successful in finding suitable hibernacula and, apparently, in foraging. This suggests that the relocation sites were adequate to meet their needs. Relocated rattlesnakes tended to hibernate ultimately in sites that were similar in overall structure and exposure to those preferred by resident rattlesnakes on the monument, suggesting that the selection of suitable hibernacula is not random (see also Reinert 1993, Sexton et al. 1992, and Gregory 1984). The presence of novel resident rattlesnakes at the dens of two relocated rattlesnakes suggests that these hibernacula possessed qualities which made them particularly suitable sites. Reinert and Zappalorti (1988a), Graves et al. (1986), and Brown and Maclean (1983) have shown that neonate rattlesnakes track adults to suitable hibernacula by following their chemical trails, and it is possible that the relocated adults used this mechanism as well to select appropriate sites. Reinert and Rupert (1995) feel that scent trailing of residents was used by relocated timber rattlesnakes in Pennsylvania to select, though not necessarily use, suitable hibernacula. Macmillian (1995) suggests that scent trails produced by a translocated population of red-sided garter snakes influenced resident snakes in the area to use a hibernaculum previously not used.

Although ingress and egress periods occurred at about the same time for control and relocated rattlesnakes, the high incidence of further hibernation site "switching" in relocated rattlesnakes compared to that of the residents suggests that initial site selection by the relocated animals may have been inappropriate. Although the winter conditions were apparently mild enough in central Arizona to permit the rattlesnakes to move to more suitable locations successfully, it is likely that these animals would not have survived such travels in a more severe climate. In a study of 20 relocated massasaugas in Ontario, Canada, Johnson (1996) found that because they could not move below the frost line, all animals either froze in the dens or were eaten by predators before emergence. Reinert and Rupert (1995) also found a higher rate of overwinter mortality in relocated rattlesnakes than in residents, and an early experiment involving translocating timber rattlesnakes to new dens also had a very high failure rate (Galligan and Dunson 1979). These results suggest that relocation of rattlesnakes will have the most dramatic negative impacts in locations where winter weather is the most severe and/or suitable hibernacula are most limited.

An extremely interesting result was that at least two rattlesnakes that returned to the monument the year after relocation used the same hibernacula and foraging sites that they had used prior to relocation. This observation adds further support to the conclusion drawn from this and other studies (e.g., Reinert 1993, Sexton et al. 1992, and Gregory 1984) that rattlesnakes exhibit strong site fidelity to suitable hibernacula and foraging areas (see also discussion of homing abilities of relocated snakes on page 77). At least one relocated rattlesnake that did not return to the monument returned to the same hibernaculum that he had first selected in the relocation area.

Changes in Activity Range Size

More than half of rattlesnakes relocated in this study increased their range size. This response is typical of many relocated animals, both in the first few months after relocation and in the subsequent year, presumably either because their basic needs are not being met, or because they are exploring to become familiar with the unfamiliar area. Increased activity range sizes have also been observed in translocated white-tailed deer (*Odocoileus virginianus*) (Jones et al. 1997), California ground squirrels (*Spermophilus beecheyi*) (Van Vuren et al. 1997), dormice (*Muscardinus avellanarius*) (Bright and Morris 1994), bullsnakes (*Pituophis melanoleucus*) (Moriarty and Linck 1995), and in timber rattlesnakes (Reinert and Rupert 1995).

A second strategy for dealing with relocation late in the activity season might be to "sit tight," conserving energy until the following year, and then begin explorations. A non-gravid female relocated rattlesnake in this study appeared to exhibit this pattern, making few movements and hibernating in close proximity to her release site. However, abruptly smaller activity ranges immediately after relocation are apparently rare.

McNally (1995) suggests that if rattlesnakes are relocated outside their normal activity range, it is likely that they will be introduced into a habitat already saturated with rattlesnakes and will move again to find a less saturated habitat. This may increase the probability of natural predation and of traffic and other human-induced mortality, increase disease transmission, and may decrease foraging and reproductive success. The population-level effects of relocation on rattlesnakes have not been addressed by any study thus far, but are obviously very important when considering the issue of relocation of any animal. Reinert (1991) observed a translocated male timber rattlesnake being courted by a previously normally-behaving resident male, which implies that the social structure of resident populations may be negatively affected by translocated snakes. Negative impacts on residents have also occurred through disease transmission in a variety of vertebrates (reviewed by Cunningham 1996, Davidson and Nettles 1992, and Dodd and Seigel 1991).

Changes in Movement Patterns

The movement patterns of rattlesnakes have been studied in detail by many researchers, including: May et al. (1996); Beck (1995); Reinert and Rupert (1995); Martin (1992); Weatherhead and Prior (1992); Duvall et al. (1990); Reinert and Zappalorti (1988b); and earlier work is summarized in Macartney et al. (1988). Four kilometers is generally the maximum straight-line distance rattlesnakes disperse from their hibernacula, and 300-700 meters is a more typical distance for western diamondbacks in Arizona (Beaupre 1995, Beck 1995). The typical movement pattern for rattlesnakes during most of the foraging season is to move long distances infrequently, making short-distance foraging movements within small patches of high concentrations of prey odor, and moving to new locations only when those patches become literally or functionally depleted (Duvall et al. 1985). Although we do not have

sufficient data to determine actual movement rates and distances for this rattlesnake population, trends in movement pattern indices for our relocated snakes after treatment are opposite those expected for free-ranging rattlesnakes.

In 1995, relocated snakes moved a greater distance per day than before treatment and also a greater distance per day than their control counterparts; they also tended to move a greater total distance and to move more frequently. These patterns of aberrant wandering movements have also been observed for other translocated western diamondbacks (Landreth 1973), timber rattlesnakes (Reinert and Rupert 1995 and Galligan and Dunson 1979), copperheads (*Agkistrodon contortrix*) (Fitch and Shirer 1971), and whipsnakes (*Masticophis taeniatus*) (Parker and Brown 1980). Wandering and even emigrating from unfamiliar habitat after translocation has been shown in a variety of species (Van Vuren et al. 1997, Compton et al. 1995, Bright and Morris 1994). Conversely, in 1996, over half of the relocated snakes did not exhibit wandering behavior.

Differences in movement parameters between control and relocated snakes compared the second year after treatment were complicated because over half of the rattlesnakes had returned to familiar areas on the monument by mid-summer and thereafter acted like resident snakes. The trend of relocated snakes to move farther than the controls the second year after relocation is not surprising given the distance covered to return to the monument, but the relocated rattlesnake that did not return also had increased movements and activity range size when compared to his original pattern. Reinert and Rupert (1995) also documented increased range sizes after translocation for those rattlesnakes that did not return to familiar surroundings.

Given the increased frequency of hibernation site "switching" in relocated snakes, we would also have expected to see a corresponding increase in the average distance moved per day while in hibernation (a reflection of mid-winter traveling). A possible explanation for this discrepancy is the significantly greater variation within the relocated group, perhaps as a result of differences in hibernation site depths or suitability between individuals, and/or inter-year variation in favorable conditions for moving between dens.

Given a trend of increased frequency of movement in the relocated snakes, the frequency of new locations used by this group might be expected to increase. They would also be expected to increase due to the observation that the longer an animal is tracked, the more likely it is to use new areas (White and Garrott 1990), as was the case for the control snakes. This was not the case for relocated rattlesnakes at Montezuma Castle: they reused sites both when in their relocation areas (due probably either to orienteering behavior or to finding suitable foraging patches), and when returned to their original activity ranges on the monument.

The directionality of movements has been studied for western diamondbacks by Landreth (1973) and for brown tree snakes (*Boiga irregularis*) by Santana-Bendix (1994). Based on their and our own field observations, we expected that the typical movement pattern for resident rattlesnakes would be random, but that

there might be some directionality for relocated rattlesnakes as they attempted to orient themselves or even returned to the monument. In fact, many of the successive movements of relocated rattlesnakes had a westerly component (although no significant bearing) in the direction that they had been moved from. One explanation for this westerly component is that the snakes were able to orient in the direction of the monument using navigational skills, and another may be the topography of the relocation area. This region is bisected by many large and small canyons which run westerly toward Wet Beaver Creek, and the area generally slopes down to the creek floodplain. Perhaps the relocated rattlesnakes followed olfactory cues (non-snake odors associated with certain biotic conditions) toward the riparian area to the west; the role of olfaction in snake ecology and orientation is discussed by Halpern (1992), Parker and Brown (1980), Klauber (1972), and Fraker (1970).

Extra-experimental effects did not appear to impact the movement patterns of the treatment groups in this study. However, some trends in these data warrant further discussion. There was a slight impact of year of the study on the frequency of movement and of new locations used by the rattlesnakes, both of which increased slightly in 1996 when compared to 1995. This may be a result of rather severe drought conditions in Arizona in 1996 (National Oceanic and Atmospheric Administration 1996), perhaps resulting in a decrease in the amount of annual biomass and seed production, possibly resulting in declines in prey populations, thereby forcing snakes to move to new foraging patches more often than they had in 1995.

Other researchers have shown that rattlesnakes, particularly males, move longer distances per day in the spring and fall months due either to migratory dispersal, and/or to increase mating opportunities (Beck 1995, Seigel 1986, Duvall et al. 1985, Landreth 1973). This was not a strong pattern at Montezuma Castle; the impact of season did not appear to be significant. There was a trend for males to move farther than females from treatment site to first hibernation site, roughly corresponding to the wet summer (monsoonal) and fall months, and a trend of increased distance moved per day during the wet summer season. These time periods roughly correspond to the onset and completion of the fall mating season for this population. Following of females by males and (presumably) guarding behavior was observed several times beginning in August and continuing through September. O'leile et al. (1994) and D. Duvall (pers. comm.) have also noticed this pattern in western diamondback populations in south-central Arizona. The directionality of snake movements during the dry summer months may be more an artifact of sampling or mere chance than a significant ecological pattern.

In general, male rattlesnakes tend to travel farther and to be more active than females, particularly gravid females, regardless of season (Brown 1991, King and Duvall 1990, Gannon and Secoy 1985). Sex differences in movement patterns between males and non-gravid females are presumably related to increased mate-searching movements by males (Duvall et al. 1992, Reinert and Zappalorti 1988b), rather than differences in foraging strategies, as King and Duvall (1990), and Duvall et al. (1990, 1985) found that males

tended to exhibit more sit-and-wait predatory behavior in foraging patches, whereas females actively explored these patches. There was a trend for males in this western diamondback population to move a greater distance per day, a greater total distance, and more frequently than females, regardless of season. Contrary to expectation, males and females did not differ in frequency of new sites used, suggesting that sex differences do not have an impact on this parameter of movement in this population.

Changes in Condition

As typical for nearly all snake species (Fitch and Pisani 1993, Klauber 1972), mass and snout-vent length were strongly correlated in this western diamondback population. Most snakes grew very little in length during the study, which is typical for mature snakes in general (Andrews 1982), and rattlesnakes in particular. Fitch and Pisani (1993) noted that western diamondbacks in Oklahoma added length and mass rapidly in their first several years, but relatively slowly once they attained reproductive maturity. Interestingly, changes in mass of individual snakes over the course of this study showed a cyclical pattern roughly corresponding to changes in season: the mass of individual snakes tended to increase through the summer foraging period, peaking just before hibernation, and then fell off during the winter, resulting in relatively lower masses when weighed early in the spring. This pattern of increasing mass during the summer foraging period and then losing mass and stored energy reserves over the winter months is typical for many reptile species in temperate climates, and is influenced by both endogenous and environmental factors (Andrews 1982). Beck (1995) and Moore (1978) found that three rattlesnakes species in southern Arizona increased foraging activity in the late summer and fall, presumably to ensure adequate energy reserves for the winter hibernation period.

There was no obvious change in condition as a result of the relocation experiment in any of the rattlesnakes, which was unexpected. This result may be due to the quality of the relocation site (relocated rattlesnakes were able to both forage and hibernate successfully in this area). Four of six relocated snakes had greatly increased distance and/or frequency of movements, and/or traveled long distances to return to the monument. We expected that these animals would lose proportionally more mass and energy than the controls, due to the increased energetic requirements associated with the wandering behavior, and would experience a decrease in the overall condition and health of the animals. This was true of one relocated snake but cannot be attributed to the effects of relocation. Loss in condition after translocation has been seen in a variety of species, including: timber rattlesnakes (Reinert 1995); giant tortoises (*Geochelone gigantea*) (Hamblen 1994); woodland caribou (*Rangifer tarandus*) (Compton et al. 1995); meadow voles (*Microtus pennsylvanicus*) (Ostfeld and Manson 1996); and kakapo (*Strigops habroptilus*) (Lloyd and Powlesland 1994). Decline in condition is most often attributed to a decrease in forage or prey availability or quality, a decrease in the overall amount of time spent foraging, and/or an increase in the amount of time spent in vigilance and/or exploring the new habitat (Wolf et al. 1996).

Year of the study did not have a significant impact on condition of these animals. This is somewhat surprising given that 1996 was an obvious drought year, and many snakes appeared to be relatively thinner that year when compared to 1996.

As expected for rattlesnakes, there was a significant effect of sex on the relationship between mass and svl, and also on the residuals of this regression. In many rattlesnakes, males tend to be longer, more muscular, and heavier than females (Beaupre 1995, King and Duvall 1990, Brown 1991, Klauber 1972, and reviewed by Shine 1993): larger, stronger males are usually able to mate successfully with more females than smaller males. In this study, these sex differences may have obscured any differences in changes in condition between relocated and control snakes, or even within each group over time. It is also interesting that there was only one suspected pregnancy in any female during the study, although courtship was observed for several different females. It would be useful to compare measurements for these females with others during the same time period to determine if this population was in exceptionally poor condition, precluding successful pregnancies. The importance of good condition to successful pregnancy has been noted for female western diamondbacks by Fitch and Pisani (1993), and for other rattlesnake species by Farrell et al. (1995) and Brown (1991).

Mortality

Increased mortality rates of displaced animals have been seen in many studies of the effects of relocation, including grizzly bears (*Ursus arctos*) (Knight and Blanchard 1997), white-tailed deer (Jones et al. 1997), ground squirrels (Van Vuren et al. 1997), and giant tortoises (Hamblen 1994). Adult rattlesnakes have few natural predators, and as a result, their mortality rates tend to be relatively low (averaging less than 20%) in habitats not impacted by humans (Reinert and Rupert 1995). In studies of the effects of relocation on rattlesnakes, however, mortality rates of displaced snakes are often three times greater than would be expected. This mortality occurs as a result of increased frequency and distance of movements, and movements at inappropriate times, which expose snakes to increased human and natural predation. McNally (1995) observed a 55 % rate of mortality, due primarily to natural and human predation (one killed by a bulldozer at a construction site); Reinert and Rupert (1995) found a 40% mortality rate for relocated timber rattlesnakes, due primarily to predation, starvation, and freezing; and as discussed earlier, Johnson (1996) found a 100% overwinter mortality rate for relocated massasaugas.

A pattern of increased mortality for relocated snakes was not seen in this study, which is to be expected, given that almost all (with the exception of Channel 34) exhibited no obvious changes in condition. While several snakes disappeared and are suspected to have succumbed to natural deaths, and two snakes died during the study, there was no obvious link between these incidents and the stress of relocation. Other studies have linked areas of heavy human activity as a main source of adult snake mortality (Hare and McNally 1997, Rosen and Lowe 1994, Seigel 1986, Galligan and Dunson 1979). The area selected for relocation of the rattlesnakes

from Montezuma Castle was chosen purposefully to have as little human impact as possible, and this selection likely contributed to the relatively high survival rate of relocated snakes in that area. This area also contained suitable hibernation and foraging areas, which probably also contributed to relatively enhanced survival rates of these snakes compared to those of other studies.

On the other hand, the only confirmed deaths during the study were those of relocated snakes. In the case of Channel 34, after returning to his original home range, it is possible that he contracted a virus (such as viperid paramyxovirus) or other disease after relocation, or that he was carrying a disease or parasite which became virulent only after the stress of being relocated to an unfamiliar area lowered his resistance (see also Cunningham 1996, McNally 1995, Davidson and Nettles 1992, Dodd and Seigel 1991, Stephenson and Pisani 1991). A necropsy could not be performed on this snake (E. Jacobson, pers. comm.). Blood samples need to be taken for the population at Montezuma Castle to determine whether such diseases or parasites exist in this population (and how they might be transmitted). The cause of mortality for the second snake is also unknown. She was discovered dead near a construction site, and it is possible that construction activities were linked to her death. A relocated rattlesnake was buried by a bulldozer in a construction site during a Tucson study of the effects of rattlesnake relocation (Hare and McNally 1997, McNally 1995).

Homing Abilities After Relocation

There appears to be a strong drive in displaced animals to return, often over huge distances, to areas with which they are familiar. For simplicity, we defined this behavior for rattlesnakes in this study as "homing," although other authors may prefer a stricter use of the term (D. Duvall and T. Sisk, pers. comm.). Over half of the rattlesnakes relocated in this study returned to the monument their second year after relocation. Other studies have also found high return rates for relocated rattlesnakes: at the Arizona-Sonoran Desert Museum in Tucson, 50% of the rattlesnakes released immediately adjacent to the museum returned, 15-20% released at 1.5 kilometers (km) returned, and at least one released at four km returned (Perry-Richardson and Ivanyi 1992). In the suburban Tucson area, several relocated rattlesnakes returned to residential locations from which they had originally been removed (McNally 1995). Homing of relocated animals is also common in other ectotherms: for example, non-migratory brown trout (*Salmo trutta*) returned over 150 meters and up a different tributary to their capture site (Halvorsen and Stabell 1990); western painted turtles (*Chrysemys picta*) returned over 8 km to their natal ponds (Orchard 1997); and whipsnakes returned over 850 meters to their hibernacula (Parker and Brown 1980).

Homing may occur because familiar locations are predictable or ideal for successful foraging, hibernating, or mating. It is likely that for animals such as rattlesnakes, which have a relatively small activity range in which they spend their whole lives and exhibit obvious site fidelity, learning of habitat parameters occurs at an early age (this hypothesis has apparently not been field-tested for snakes, but its potential importance is mentioned by Heatwole

[1977] and Reinert [1993]). It is possible at Montezuma Castle that the riparian area and heavily-used areas of human activity may artificially increase prey populations (see also Graham 1991), and in combination with suitable hibernacula on the monument, might be a particularly ideal area for rattlesnakes. This suitability alone, as well as the presence of other rattlesnakes, would encourage the return of rattlesnakes that were relocated from the monument if the relocation area did not contain equally suitable areas for foraging or hibernating. The relative abundance of prey was not compared between the relocation site and the monument, but such a study would address this issue.

Although it might be suggested that the relocated rattlesnakes returned to the monument because they were already familiar with the relocation sites, there is no evidence supporting this hypothesis. In three seasons of study, no rattlesnake was ever observed to travel more than one kilometer in a straight line during the course of its active season, so it is unlikely that any of them would have traveled to or from the relocation area prior to the experiment. Also, most snakes exhibited some altered behavior in the relocation sites, and did not return to the monument immediately after relocation.

It is likely that snakes which returned spent some time orienting within the relocation site before finding potential return routes to their original activity range, although the mechanisms that they used are not known. In general, the mechanisms that snakes use to orient and navigate are not known. It is thought that they use a combination of celestial (sun compass and polarized light), landmark, and olfactory cues, along with internal "clocks" to navigate, usually between hibernacula and foraging sites (Halpern 1992, Lawson 1991, Graves et al. 1986, Gregory 1984, Parker and Brown 1980, Newcomer et al. 1974, Landreth 1973, Fraker 1970). There is also increasing speculation that the facial pits are capable of detecting long-distance radiant heat emissions, which could be used in navigation (Sexton et al. 1992, Berson and Hartline 1988). If this is true, then the large limestone outcrop in which many residents hibernated would be an obvious landmark: these cliffs are routinely several degrees Celsius warmer than the surrounding landscape during the day, and emit discernible radiant heat during summer nights (pers. obs.). Perhaps the snakes oriented toward this landmark. Or perhaps the snakes simply followed the slope of the land and/or olfactory cues toward the riparian area west of the relocation sites: at least two of the relocated rattlesnakes followed one particularly large east-west running wash to enter the monument the second year after relocation. Another possibility is that these rattlesnakes followed the scent trails of unknown rattlesnakes to the monument (see also Reinert and Zappalorti 1988a, Ford 1986, Graves et al. 1986), although King et al. (1983) found that at least some adult prairie rattlesnakes did not use scent-trailing as an orientation mechanism.

Not only did the relocated snakes return to the monument, they returned to the activity ranges that they had used before relocation, and to the exact same retreat or foraging sites and hibernacula that they had used prior to relocation. Homing to exact locations has also been seen in other rattlesnakes (Hare and McNally

1997, Perry-Richardson and Ivanyi 1992), and in whipsnakes, racers (*Coluber constrictor*), and bullsnakes (Parker and Brown 1980). Although it is possible that the returned rattlesnakes were found in the exact same areas by chance (Ostfeld and Manson 1996), it is more likely that they were using the same cues to seek out suitable sites that they had used before, or perhaps relying on some internal "map" in combination with familiar structural or thermal landmarks (Sexton et al. 1992, Newcomer et al. 1974).

There appears to be individual variation in the drive or success in returning to a familiar area, given that not all of the rattlesnakes returned to the monument. This pattern has also been seen in other studies of relocation, where it has been tied to social factors and distance of displacement, including those on whipsnakes (Parker and Brown 1980), white-tailed deer (Jones et al. 1997), ground squirrels (Van Vuren et al. 1996), and dormice (Bright and Morris 1994). It is likely that these snakes did not return because they were able to meet all of their needs adequately in the relocation area: they were frequently located within the riparian area north of the monument, where they exhibited normal foraging behavior, and they found suitable hibernacula. One of these snakes, a female, was observed mating with a resident male near her relocation site a few weeks prior to entering hibernation in 1996. The outcome of this mating was not determined, but it is significant because it showed that normal mating behavior was not impacted by the stress of relocation, at least for this particular animal.

The ability of relocated western diamondback rattlesnakes to travel long distances to return to a familiar area after intentional displacement is a particularly important finding of this study. Other studies of rattlesnake relocation in the southwest have also concentrated on this species. For many other southwestern rattlesnake species, the effects of relocation are not known, and even basic information about natural history and movement patterns is lacking. However, it is likely that a homing ability is present in other rattlesnake species as well, suggesting that relocation is not an effective management tool for decreasing rattlesnake-human interactions in national park or other public areas.

Other Considerations

There are other important issues surrounding the relocation of rattlesnakes that should be addressed in future research. What are the impacts of translocations on resident rattlesnakes in the relocation area, particularly when large numbers of rattlesnakes are continuously displaced to the same area? What are the ecological impacts of rattlesnake relocation (i.e., impacts on rattlesnake predators, prey, and species occurring sympatrically)?

Finally, there is an issue apart from scientific research: what role could public education about rattlesnakes play in diminishing the need for such relocation programs? In three years of talking with the staff and general public at Montezuma Castle National Monument, we found a general lack of understanding of the life history of rattlesnakes, and much-exaggerated beliefs about the danger posed by rattlesnakes and their defensive behavior. This lack of basic understanding of rattlesnakes, perhaps combined

with innate, genetic disposition toward fear of snakes in some individuals, has led to wide-spread mistrust and persecution of these animals (see also Wilson 1996, Greene 1997).

This fear, combined with misunderstanding of the factors potentially influencing rattlesnake distribution, has led to the expectation among many visitors at Montezuma Castle (pers. comm.) that rattlesnakes will be removed from or killed in areas where they are likely to come into contact with humans, including national parks (see also Hare and McNally 1997). However, it is important to point out to the general public that a majority of southwestern national parks have had minimal snakebites in the last 25 years (see Table 1). Also, anywhere from 50-75% of all venomous snakebites in the United States are "illegitimate"; they occur after victim recognizes that he or she is interacting with a venomous snake, and proceeds to provoke the snake (Dart et al. 1992, Curry et al. 1988, Hardy 1986). A majority of the snakebites

occurring in national parks are of this nature, suggesting that discouraging handling of rattlesnakes should be emphasized.

In our interactions with the general public, we have seen that when people are educated about rattlesnake behavior, roles in the ecosystem, the true incidence of snakebite, and of park mandates to protect natural resources, their attitudes are often changed. Interest in rattlesnakes in the first place is often due primarily to fear and misinformation; once educated, people become much more tolerant of rattlesnakes, less likely to expect their removal, and more likely to encourage protection of the animals. Thus, public education campaigns to educate people in the southwest about rattlesnakes could help to reduce the desire for long-distance relocation of rattlesnakes.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

To understand potential impacts of relocation on any species, we first need to understand their basic biology. An important finding of this study was that this population of western diamondbacks at Montezuma Castle National Monument shows very high site fidelity, both to hibernacula and to foraging locations. Snakes in this population, given a choice, did not disperse more than one kilometer in a straight line from their hibernacula during the summer foraging months. Some individuals followed almost the exact same migratory routes to access and disperse from their dens, year after year. Given these fixed and generally predictable behavioral patterns, it is possible that displacement of a rattlesnake from this system into a habitat which was unsuitable for either hibernating or foraging could have negative consequences on its foraging ability, reproductive success, and/or general survival.

Relocation of rattlesnakes two kilometers from Montezuma Castle, however, resulted in few statistically significant impacts on rattlesnake movement patterns or behavior. There were obvious trends in the response of snakes to the treatment: more than half of the relocated snakes exhibited wandering behavior after relocation, and this response has also been seen in other studies of the effects of relocation on rattlesnakes. Given this, and taking into consideration the low sample size for many statistical analyses, it is possible that the finding of few significant impacts is due more to the low power of the statistical tests to detect differences than to a true lack of effects on relocated rattlesnakes. Displacement of rattlesnakes from Montezuma Castle did not result in significant changes in the overall health or mortality of the relocated snakes, and this result is contrary to other rattlesnake relocation studies. This discrepancy may be due to the relative paucity of human activity and to suitable hibernacula and foraging areas in the relocation area, and to the continuity of such suitable habitat between the relocation area and the monument.

Although responses to the relocation experiment varied between individuals, more than half of the relocated western diamondback rattlesnakes returned to the monument. The ability of rattlesnakes to return over long distances to their original activity ranges after being displaced suggests that relocation is not an effective long-term management tool for decreasing rattlesnake-human interactions in national park or other public areas.

There are several other important management implications of this research (see also "Guidelines for Rattlesnake Management" in Appendix B). When dealing with nuisance rattlesnakes in public use situations or even around private homes, the first and most important question to be addressed is the reason for rattlesnake presence in the area. If the area has a relatively higher concentration of rattlesnake prey due to human activities or modifications of the landscape, or is near suitable hibernacula, then such an area is likely very attractive to rattlesnakes. Continuously relocating individual snakes from these areas is not going to decrease the number of rattlesnakes in the area: more snakes will simply immi-

grate to take advantage of the concentrated prey base or the hibernacula, and snakes that are relocated are likely to return if possible. As well, rattlesnakes foraging frequently near or in concentrated human use areas may be habituated to the presence of people, and thus perhaps less likely to display defensive behaviors than newly arrived unhabituated snakes. We found that the rattlesnakes at Montezuma Castle tended to rely heavily on procrystis, rarely rattled when approached, and did not strike unless handled. Thus, unless inadvertently stepped on or handled, rattlesnake presence per se near visitor trails and the housing area at Montezuma Castle poses a minimal threat to public safety.

One long-term solution to rattlesnake-human conflicts in these areas would be to make these microhabitats less attractive to rattlesnake prey and, therefore, less attractive to rattlesnakes during the foraging season. On the other hand, if the area is near suitable hibernacula, two feasible ways to solve potential conflicts would be to physically re-route rattlesnakes around human use areas (provided the snakes are not cut off from their dens or forced onto roadways), or to re-route people from the migratory paths of the snakes (i.e., by creating elevated walkways for visitors).

Another feasible option is short-distance relocation of individual snakes into suitable habitat, preferably less than 50 meters, from their capture point. To discourage wandering behaviors, no snake should be relocated farther than one kilometer (no snake voluntarily dispersed more than this distance from its hibernation site). Relocation should always occur away from heavily-used roads into habitats similar to that from which the rattlesnake was displaced. This is particularly important for species which are more specialized in their habitat requirements, such as sidewinders (*C. cerastes*) (e.g. Secor 1994). In this scenario, snakes are simply removed from trails or from proximity to buildings into adequate vegetative cover, where they are likely to continue their travels without again encountering humans. This relocation is most effective when in the direction of the snake's likely travel path, particularly during migration periods: toward potential hibernacula in the fall (after early October) and away from these sites in the spring (after early April). At Montezuma Castle, snakes should be moved to the outcrops west of the visitor trails in fall and toward Wet Beaver Creek east of the trails in spring.

Although this study did not show significant negative impacts of relocation on rattlesnakes, other similar studies have shown high mortality rates due to wandering behaviors, unsuitable habitat, and increased contact with predators (particularly human predators). Further, because this study has demonstrated that rattlesnakes are capable of homing over long distances, long-distance relocation of rattlesnakes should not be used to manage potential rattlesnake-human interactions.

Instead, the most effective long-term solution to rattlesnake-human conflicts will likely be education: raising people's awareness and understanding of snakes. A focus by national park

areas on environmental education will also become more and more important as available habitat outside park and other public refuges shrinks and rattlesnake populations become increasingly threatened. To encourage visitors and staff to respect rattlesnakes, and to

discourage illegitimate bites, it is important to educate them about rattlesnake behavior, rattlesnakes' important roles in the ecosystem, of the true incidence of snakebite, and of federal and state mandates to protect natural resources.

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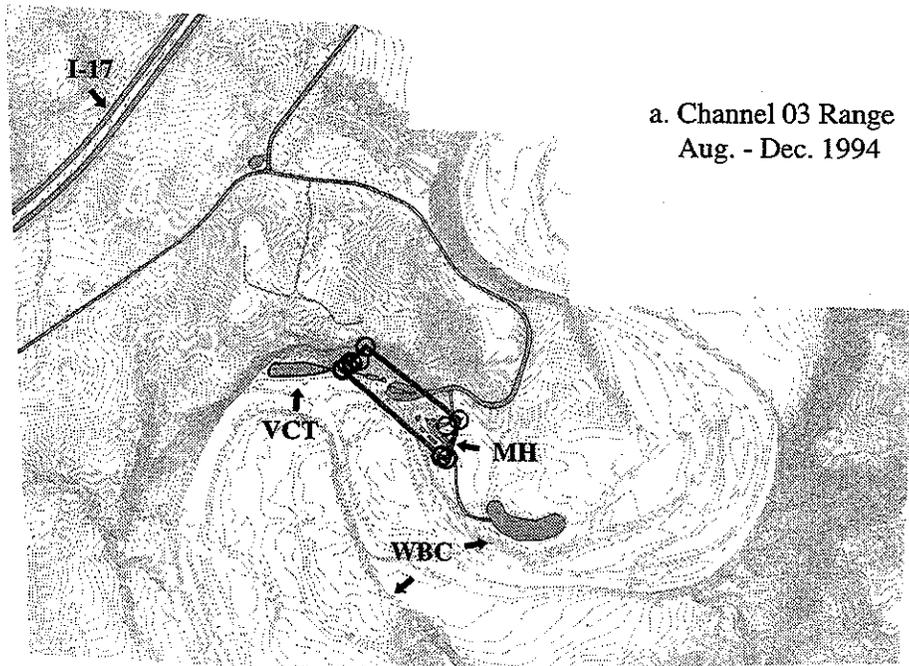
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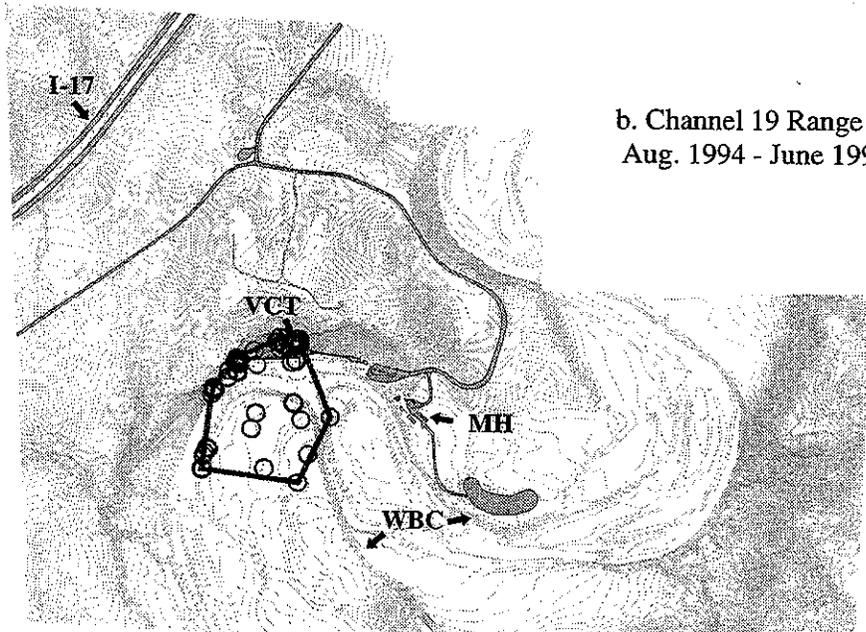
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APPENDIX A

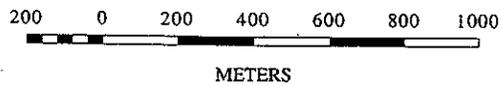
LOCATIONS AND ACTIVITY RANGES FOR
19 TELEMETERED ADULT WESTERN DIAMONDBACKS
AT
MONTEZUMA CASTLE NATIONAL MONUMENT,
AUGUST 1994 - DECEMBER 1996



a. Channel 03 Range
Aug. - Dec. 1994



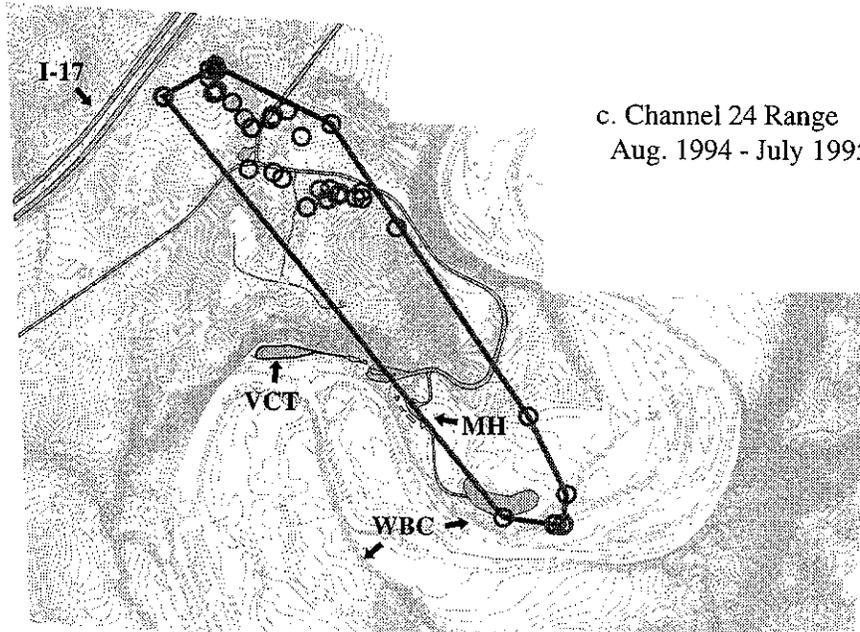
b. Channel 19 Range
Aug. 1994 - June 1995



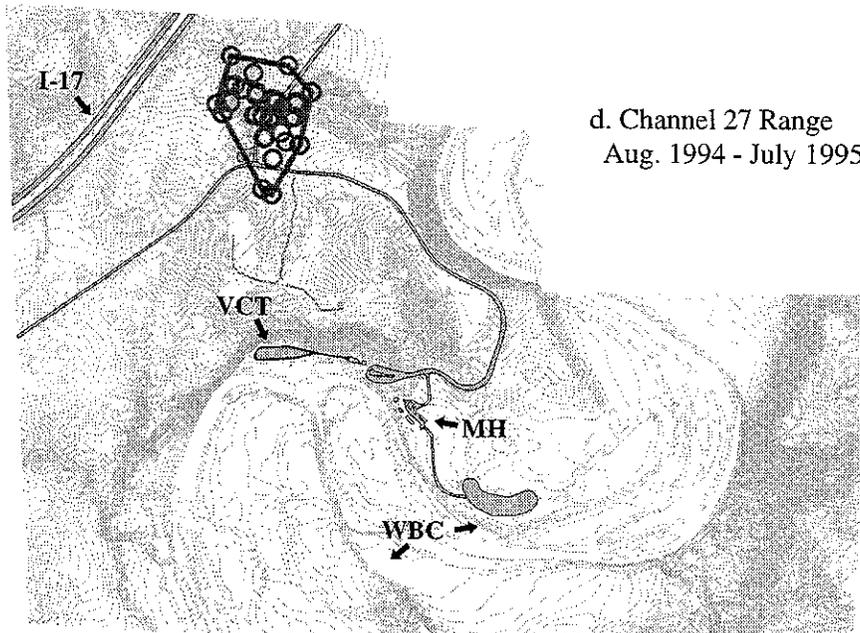
 Activity Range and Locations



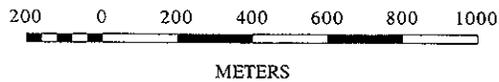
Figure 22 a. and b. Activity range (estimated by the minimum convex polygon method) and locations for two non-experimental western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, between August 1994 and July 1995. a. Channel 03, male. b. Channel 19, female. Open circles represent one location of each snake; solid lines outline activity range. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.



c. Channel 24 Range
Aug. 1994 - July 1995



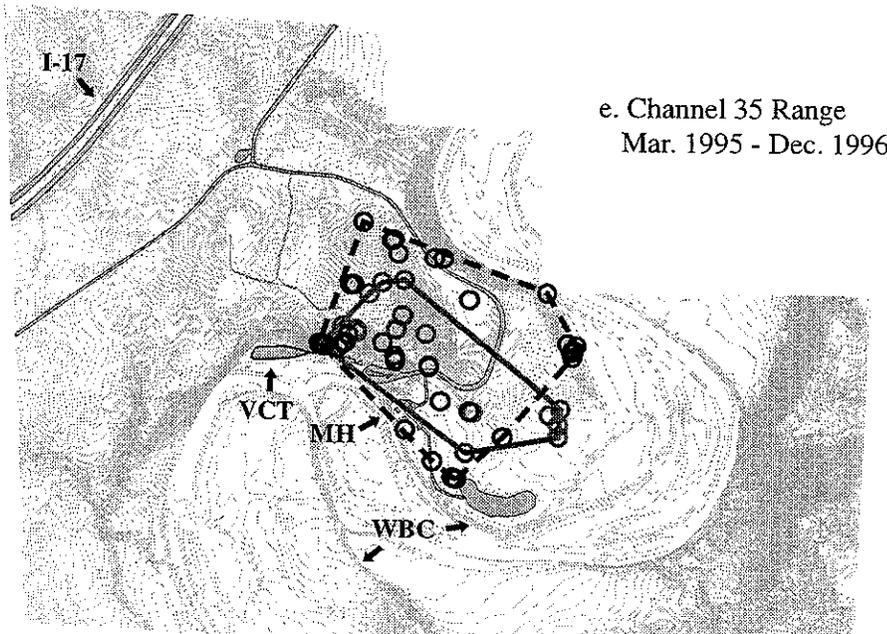
d. Channel 27 Range
Aug. 1994 - July 1995



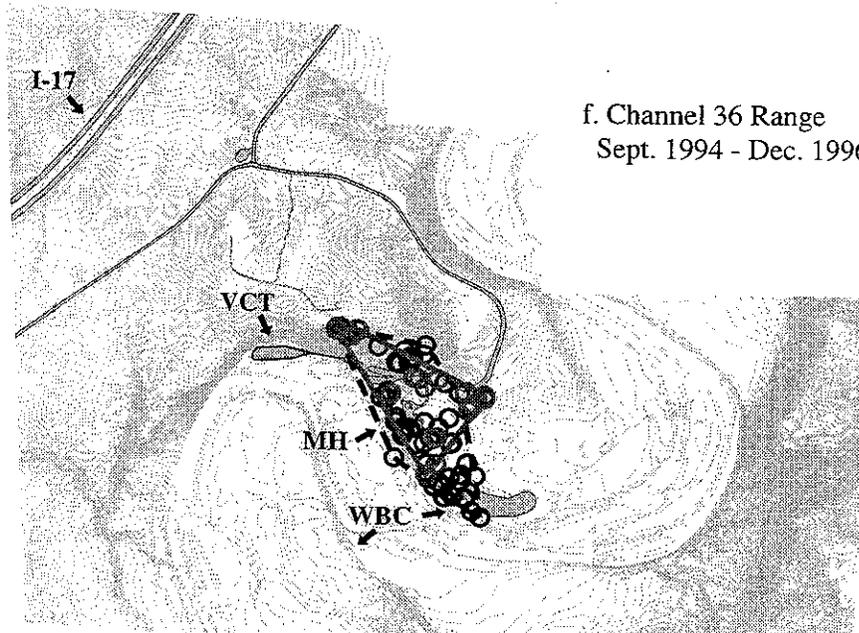
 Activity Range and Locations



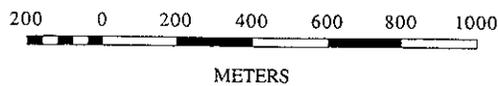
Figure 22 c. and d. Activity range (estimated by the minimum convex polygon method) and locations for two non-experimental western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, between August 1994 and July 1995. c. Channel 24, female. d. Channel 27, female. Open circles represent one location of each snake; solid lines outline activity range. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.



e. Channel 35 Range
Mar. 1995 - Dec. 1996



f. Channel 36 Range
Sept. 1994 - Dec. 1996



-  Activity Range and Locations Before Treatment
-  Activity Range and Locations After Treatment



Figure 22 e. and f. Activity range (estimated by minimum convex polygon) and locations for two control western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, between September 1994 and December 1996. e. Channel 35, male. f. Channel 36, female. Each underwent handling treatment in August 1995 (see Methods). Open circles are one location of each snake; solid lines outline activity range before treatment; and dashed lines outline range after. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center trails, WBC = Wet Beaver Creek.

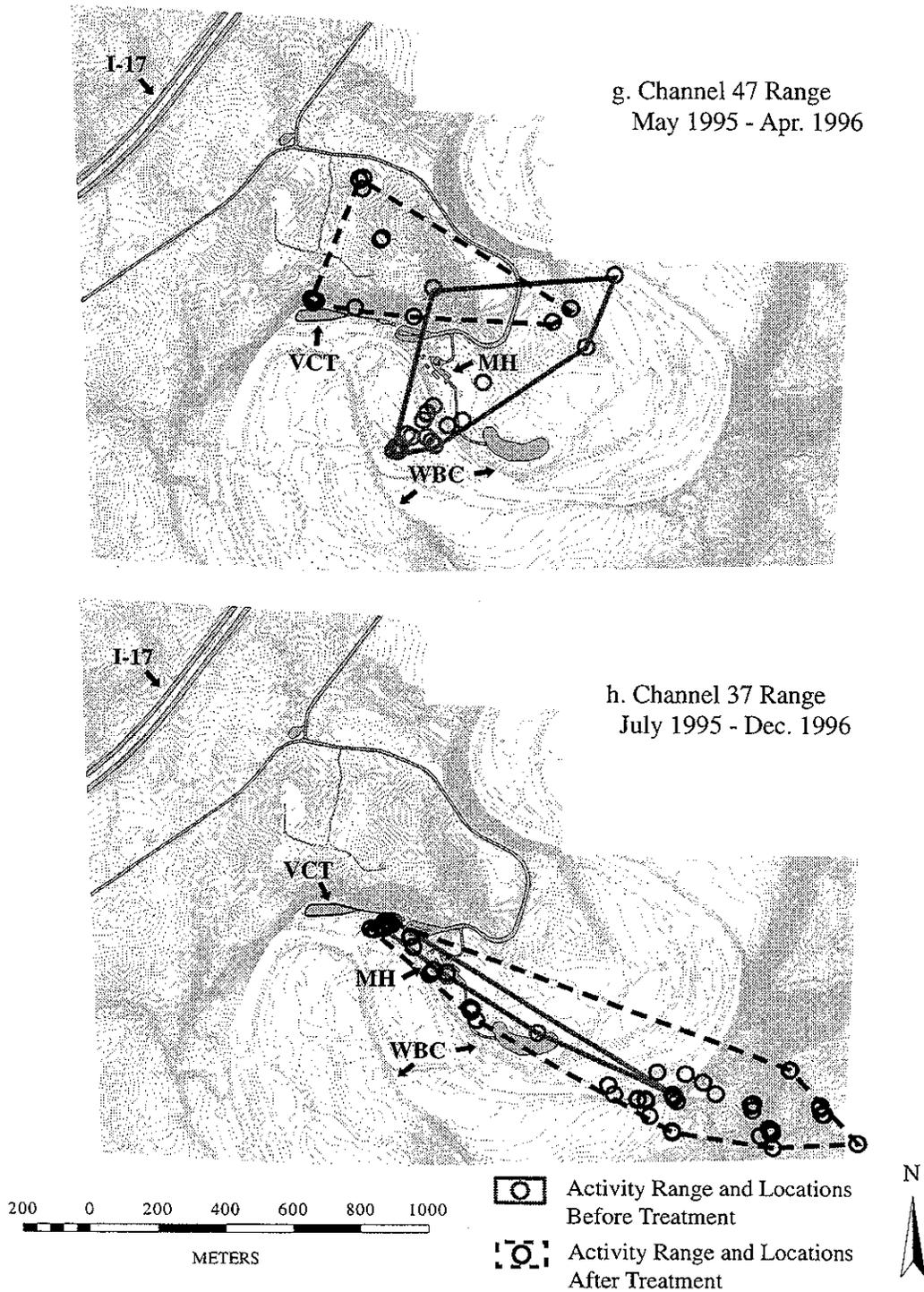
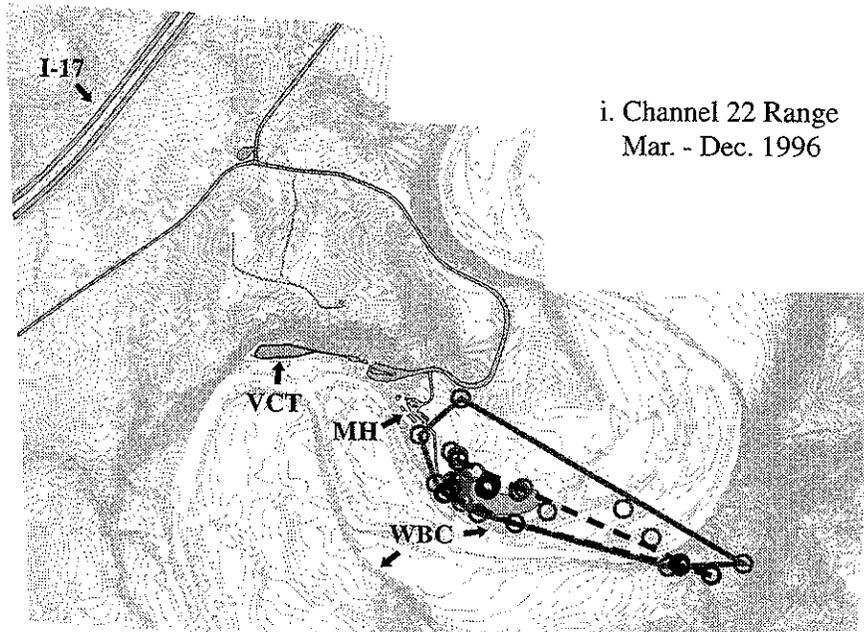
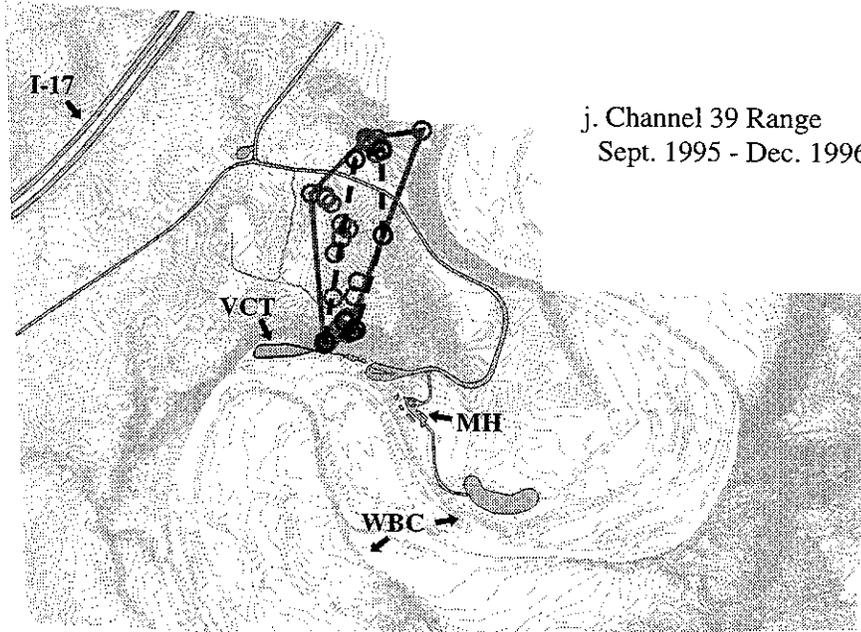


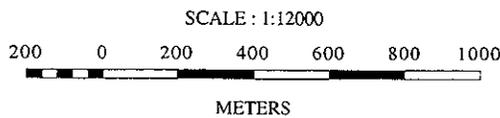
Figure 22 g. and h. Activity range (estimated by minimum convex polygon) and locations for two control western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, between May 1995 and December 1996. g. Channel 47, male. h. Channel 37, male. Each underwent handling treatment in August 1995 (see Methods). Open circles are one location of each snake; solid lines outline activity range before treatment; and dashed lines outline range after treatment. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.



i. Channel 22 Range
Mar. - Dec. 1996



j. Channel 39 Range
Sept. 1995 - Dec. 1996



-  Activity Range and Locations Before Treatment
-  Activity Range and Locations After Treatment



Figure 22 i. and j. Activity range (estimated by the minimum convex polygon method) and locations for two control western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, between September 1995 and December 1996. i. Channel 22, female. j. Channel 39, female. Each was given handling treatment in August 1996 (see Methods for experiment description). Open circles are one location of each snake; solid lines outline activity range before treatment; and dashed lines outline range after treatment. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

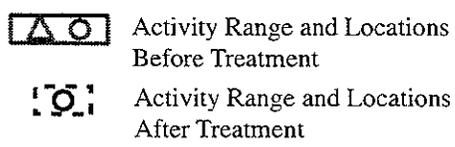
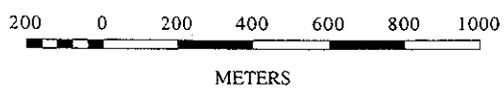
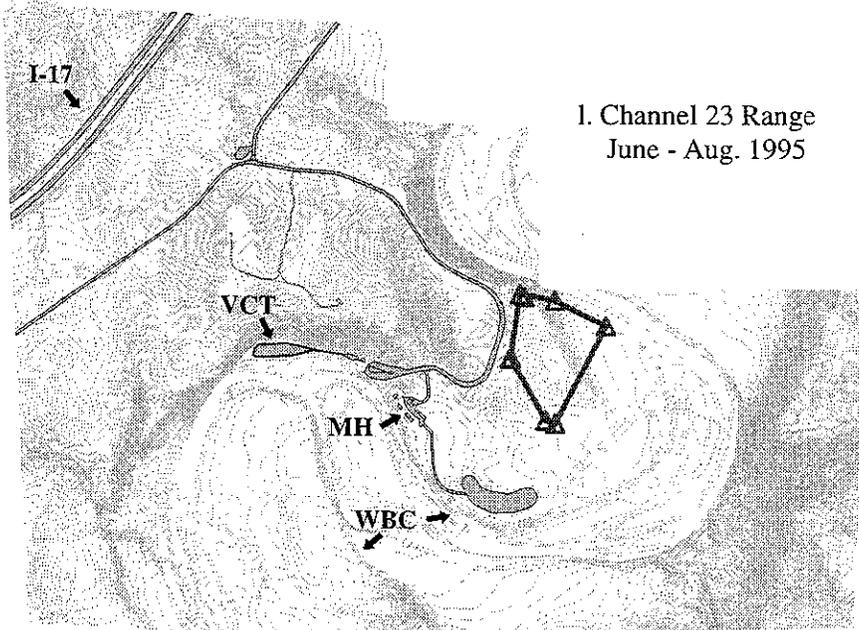
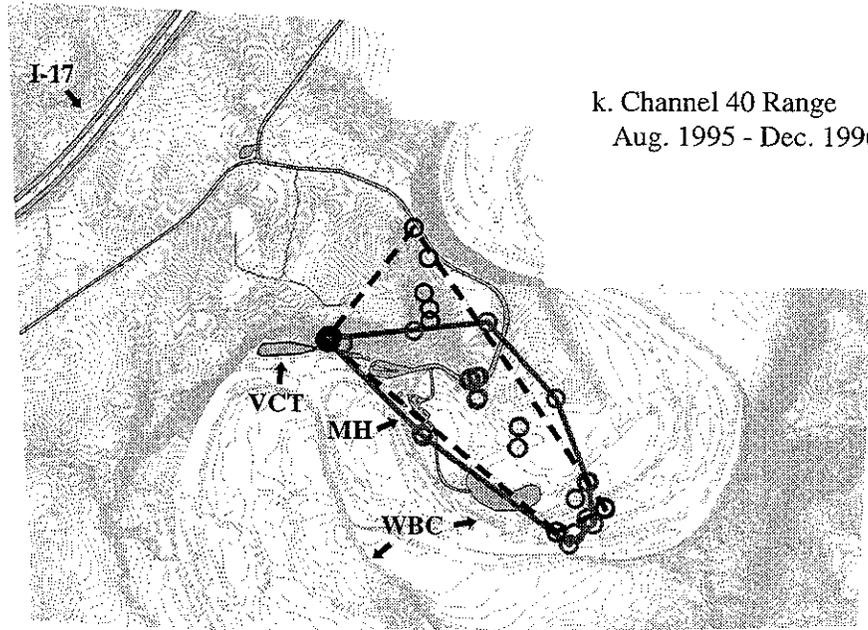
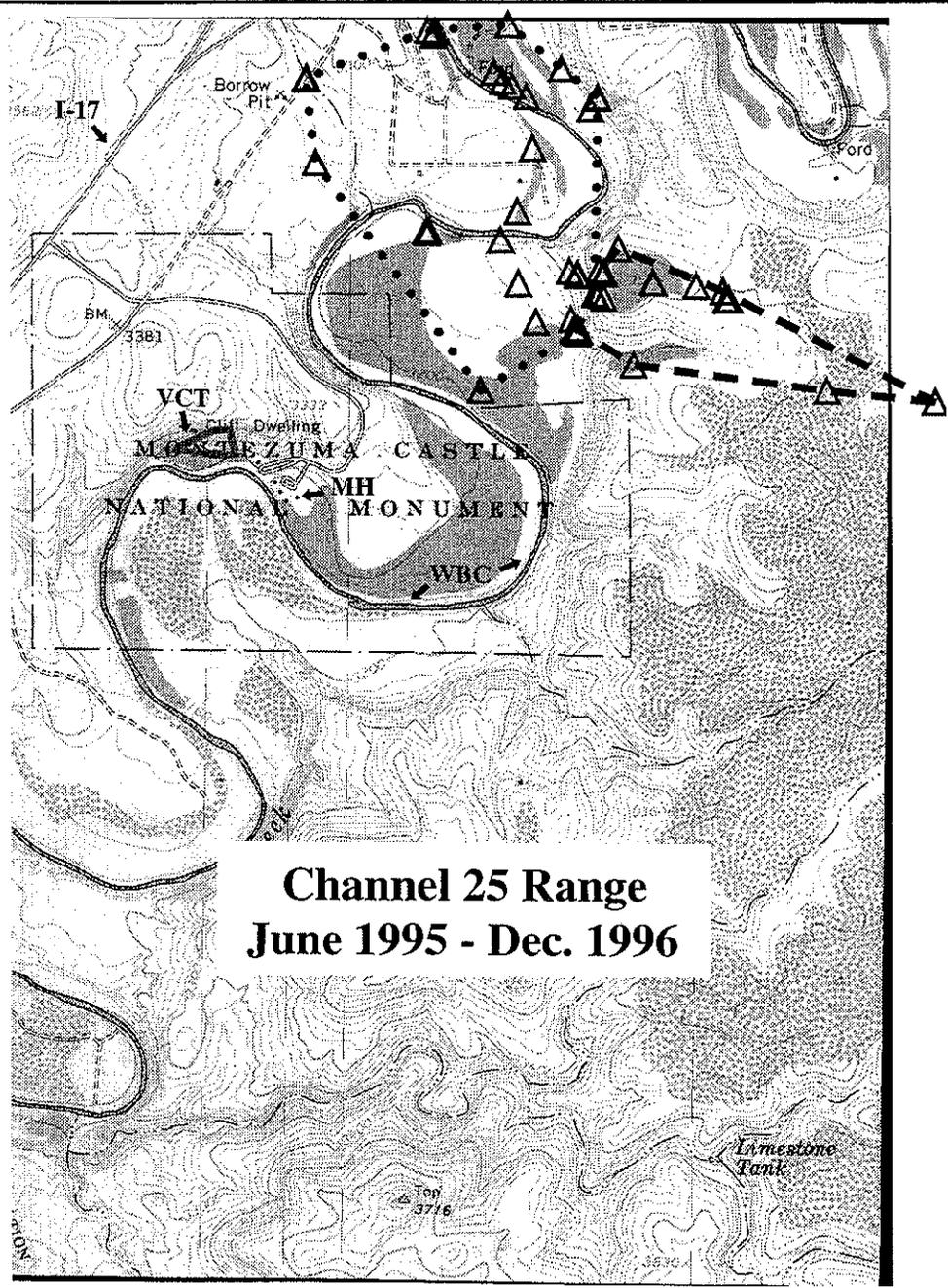


Figure 22 k. and l. Activity range (estimated by minimum convex polygon) and locations for two western diamondback rattlesnakes at Montezuma Castle National Monument, Arizona, between June 1995 and December 1996. k. Channel 40, male, control, handling treatment in August 1996. l. Channel 23, female, relocated, relocation in August 1995 (lost, see text). Open circles and triangles are one location of each snake; solid lines outline activity range before treatment; dashed lines outline range after treatment. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.



**Channel 25 Range
June 1995 - Dec. 1996**

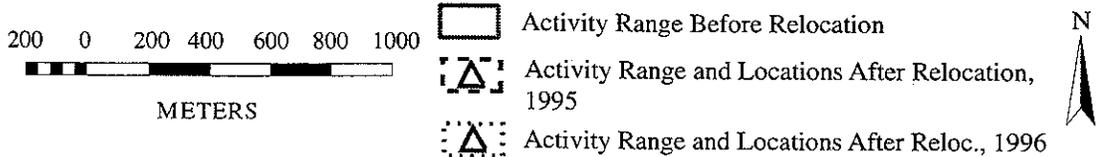


Figure 22m. Activity range (estimated by the minimum convex polygon method) and locations for Channel 25, male western diamondback rattlesnake at Montezuma Castle National Monument, Arizona, between June 1995 and December 1996. Relocation at two km from the Monument occurred in August 1995 (see Methods). Open triangles are one snake location; solid lines outline activity range before relocation; dashed lines outline 1995 range after relocation; dotted lines outline 1996 range. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center trails, WBC = Wet Beaver Creek.

Channel 34 Range July 1995 - Dec. 1996

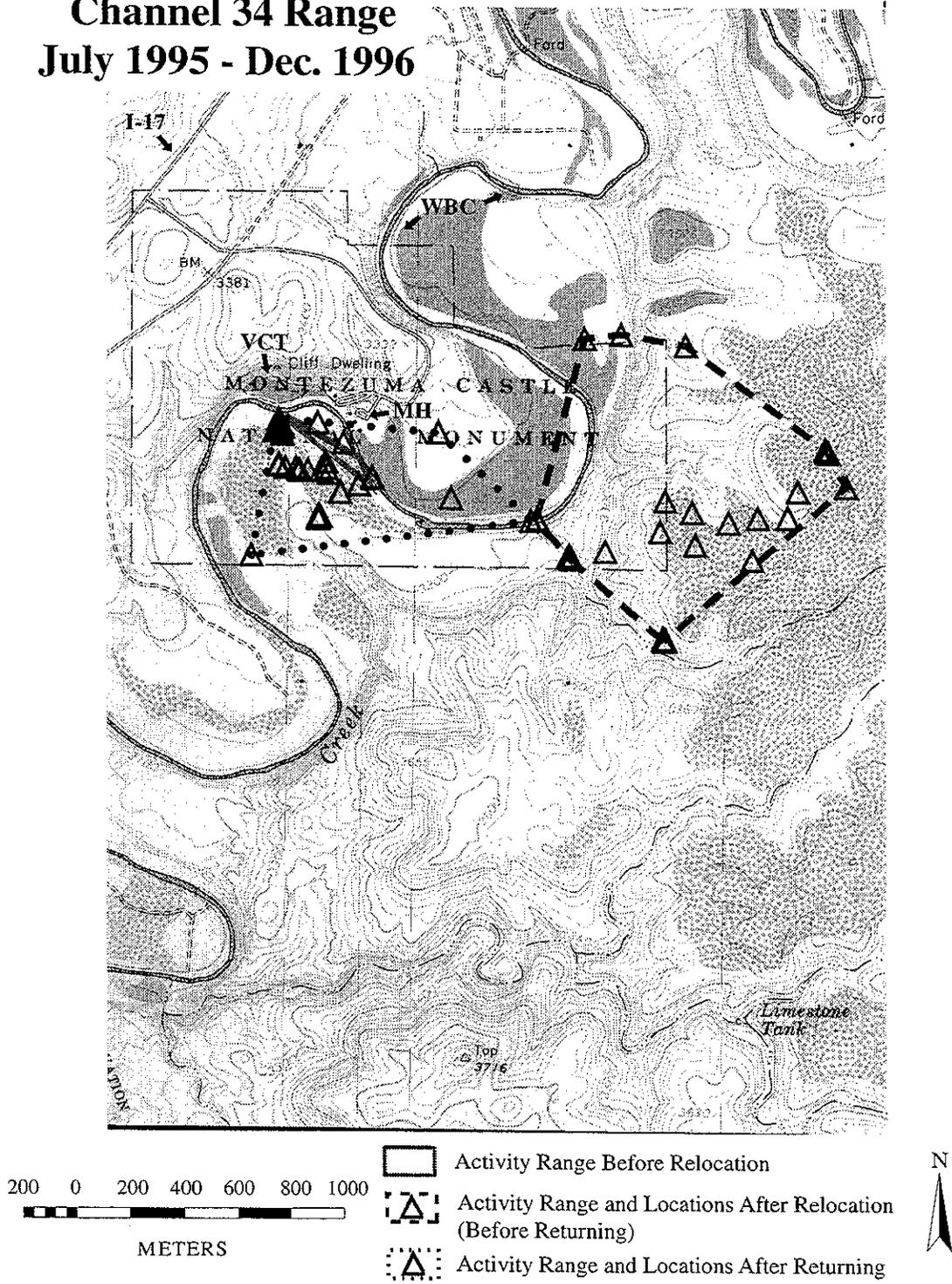


Figure 22n. Activity range (estimated by minimum convex polygon) and locations for Channel 34, male western diamondback rattlesnake at Montezuma Castle National Monument, Arizona, between July 1995 and December 1996. Relocation at two km from the Monument occurred in August 1995 (see Methods). Open triangles are one location of the snake; solid lines outline activity range before treatment; dashed lines outline range after treatment; dotted lines outline range after returning. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center trails, WBC = Wet Beaver Creek.

Channel 41 Range Oct. 1994 - Dec. 1996

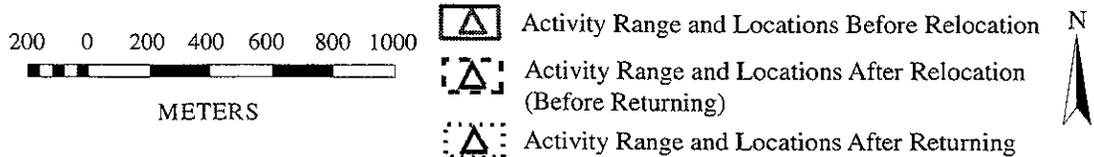
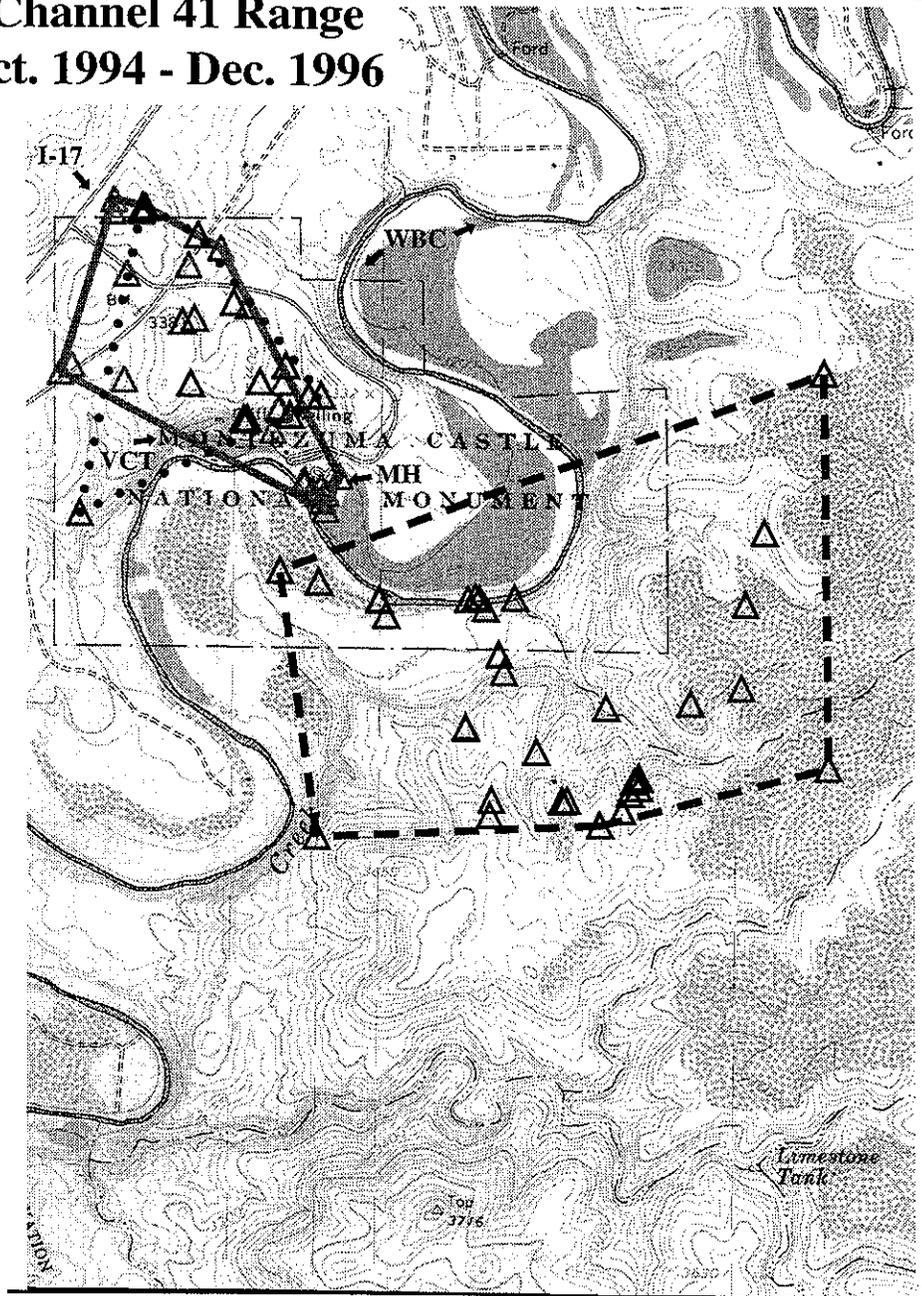
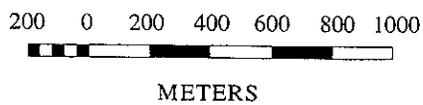
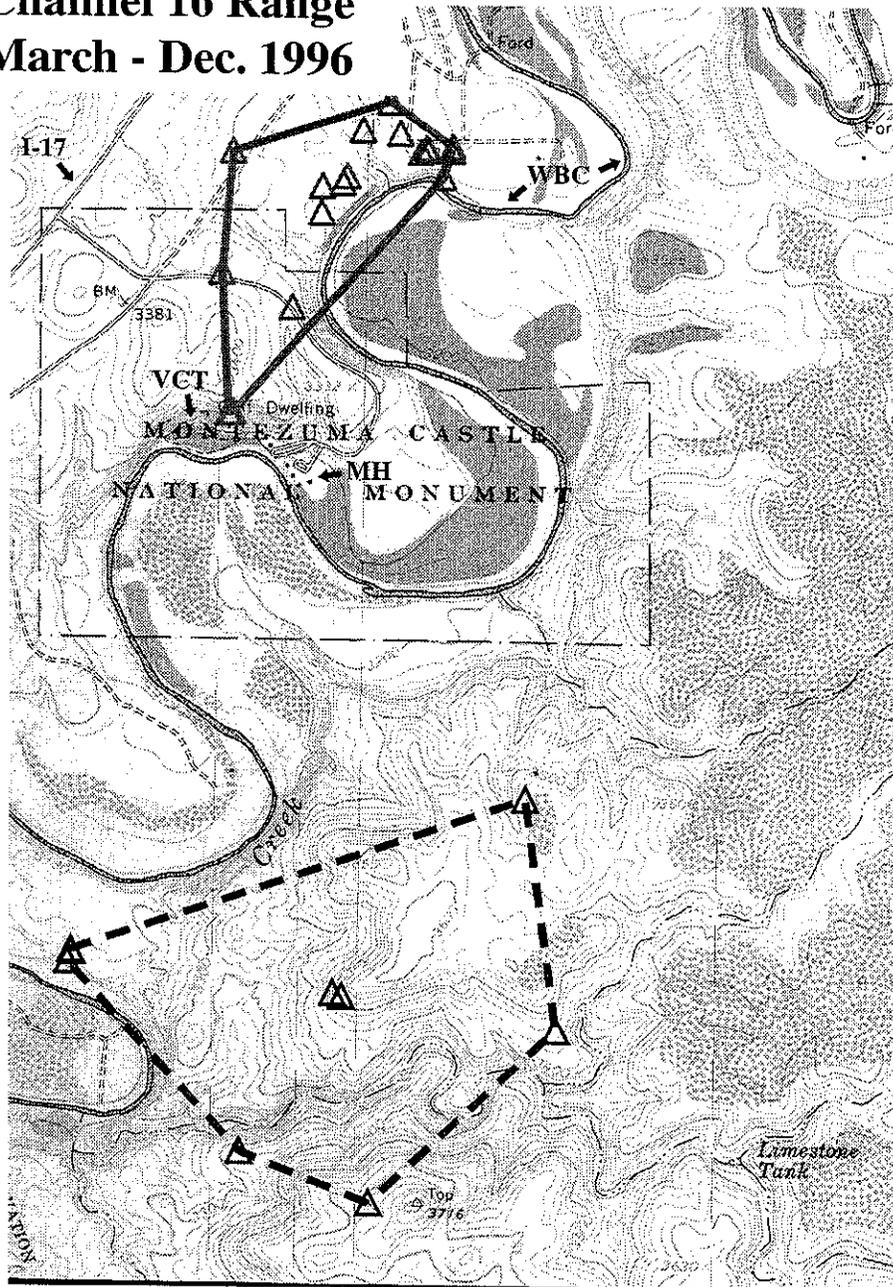


Figure 22o. Activity range (estimated by minimum convex polygon) and locations for Channel 41, male western diamondback rattlesnake at Montezuma Castle National Monument, Arizona, between October 1994 and December 1996. Relocation at two km from the Monument occurred in August 1995 (see Methods). Open triangles are one location of the snake; solid lines outline activity range before treatment; dashed lines outline range after treatment; dotted lines outline range after returning. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center trails, WBC = Wet Beaver Creek.

Channel 16 Range March - Dec. 1996



Activity Range and Locations Before Relocation



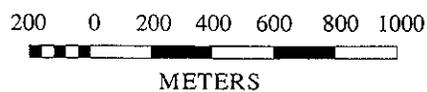
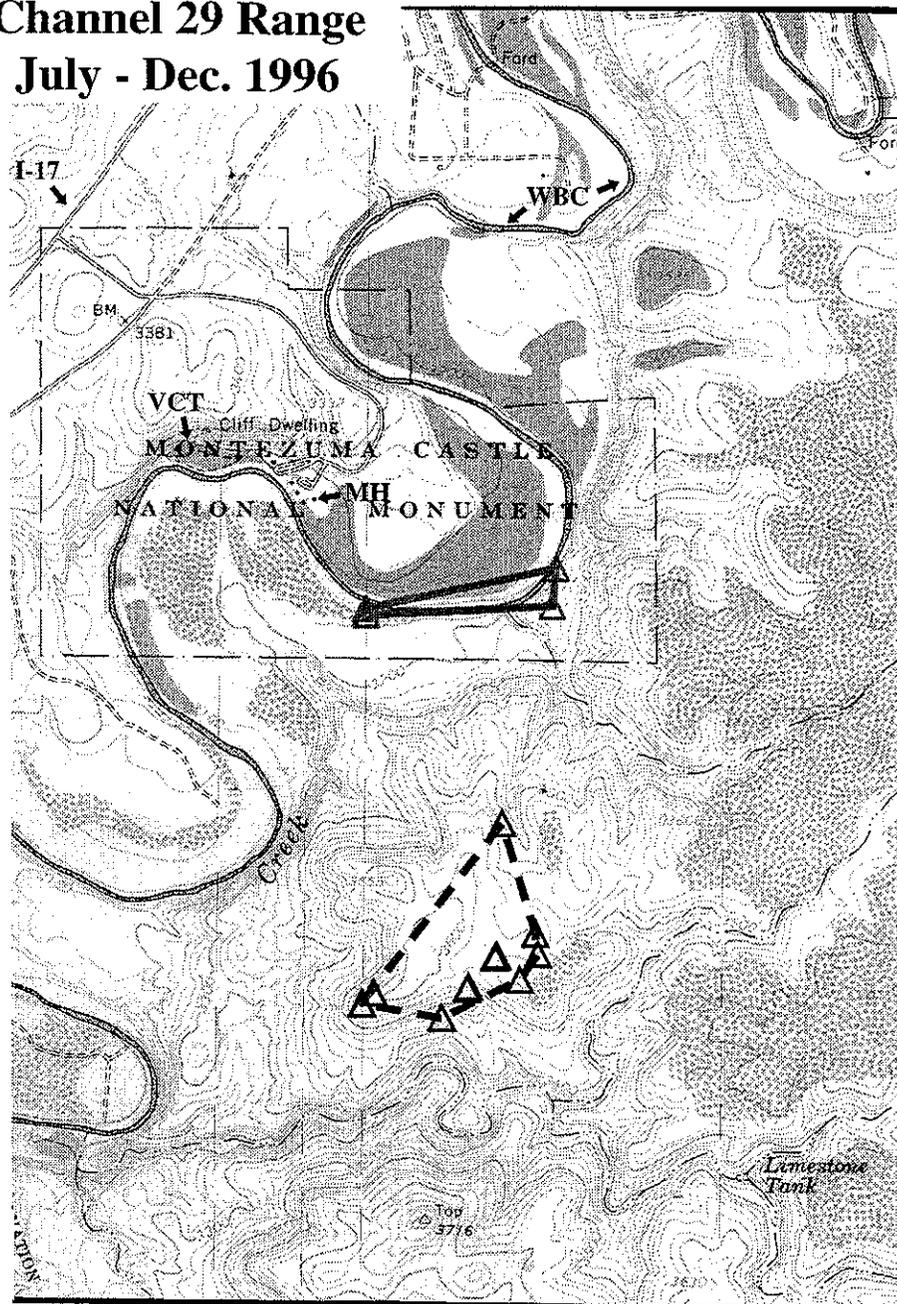
Activity Range and Locations After Relocation

N



Figure 22p. Activity range (estimated by the minimum convex polygon method) and locations for Channel 16, male relocated western diamondback rattlesnake at Montezuma Castle National Monument, Arizona, between March and December 1996. Relocation at two km from the Monument occurred in August 1996 (see Methods for description). Open triangles are one location of the snake; solid lines outline activity range before treatment; dashed lines outline range after treatment. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

Channel 29 Range July - Dec. 1996

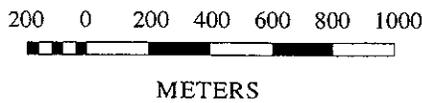
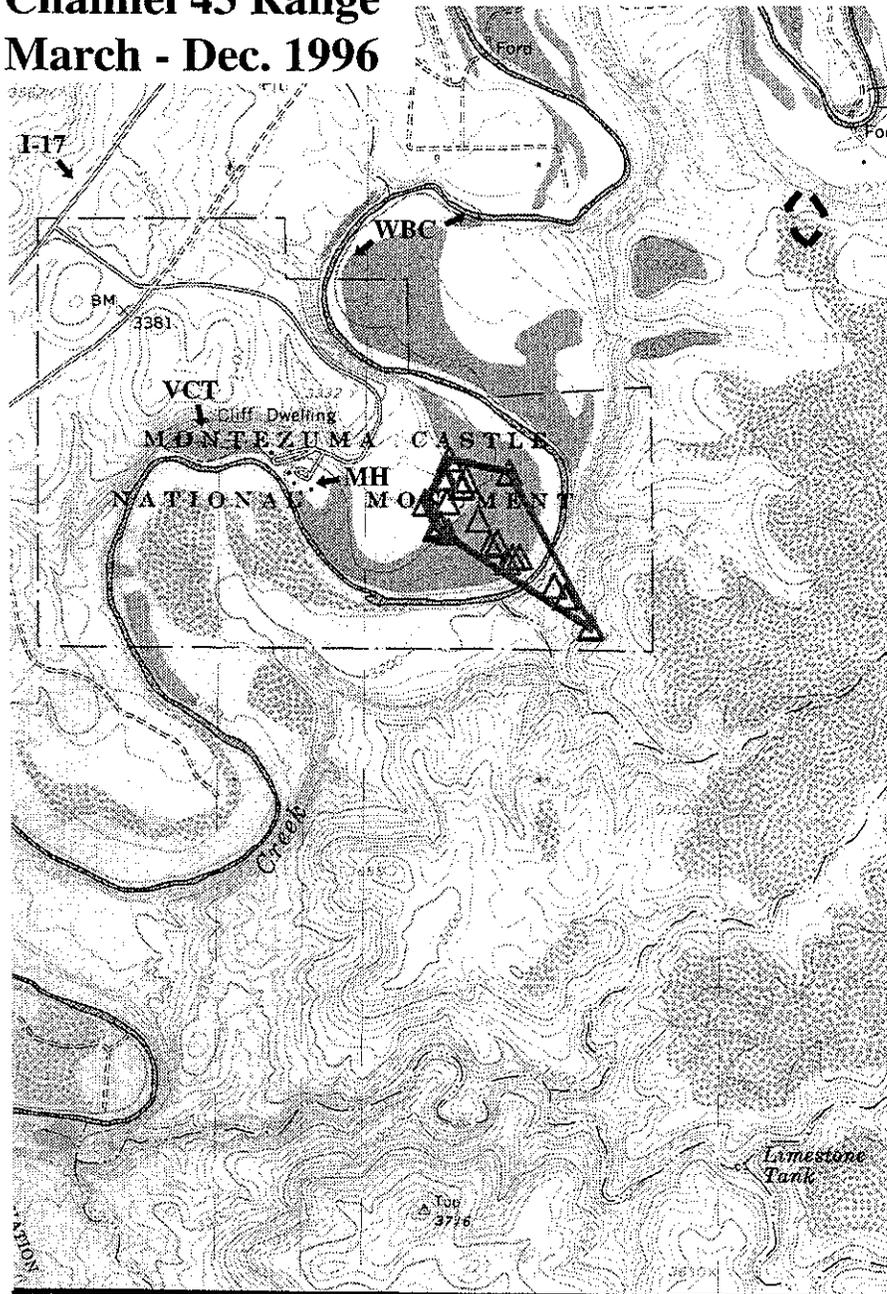


 Activity Range and Locations Before Relocation
 Activity Range and Locations After Relocation



Figure 22q. Activity range (estimated by the minimum convex polygon method) and locations for Channel 29, male relocated western diamondback rattlesnake at Montezuma Castle National Monument, Arizona, between July and December 1996. Relocation at two km from the Monument occurred in August 1996 (see Methods for description). Open triangles are one location of the snake; solid lines outline activity range before treatment; dashed lines outline range after treatment. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

**Channel 43 Range
March - Dec. 1996**



Activity Range and Locations Before Relocation



Activity Range After Relocation



Figure 22r. Activity range (estimated by the minimum convex polygon method) and locations for Channel 43, female western diamondback rattlesnake at Montezuma Castle National Monument, Arizona, between March and December 1996. Relocation at two km from the Monument occurred in August 1996 (see Methods for description). Open triangles are one location of the snake; solid lines outline activity range before treatment; dashed lines outline range after treatment. I-17 = Interstate 17, MH = staff housing area, VCT = visitor center area trails, WBC = Wet Beaver Creek.

APPENDIX B

**GUIDELINES FOR RATTLESNAKE MANAGEMENT
AT MONTEZUMA CASTLE NATIONAL MONUMENT**

GUIDELINES FOR RATTLESNAKE MANAGEMENT AT MONTEZUMA CASTLE NATIONAL MONUMENT

I. Human and Rattlesnake Safety

- A. All park staff should be trained in first aid procedures, and the park should have extractor kits and other necessary medical supplies, as well as a plan for proper care of snakebite victims.
- B. All personnel should receive training in proper handling and transportation of venomous snakes, to decrease risk of injury to both snakes and people.
1. Rattlesnakes should not be handled unless they are posing an immediate or potential future threat to human safety. Snakes that are hidden or moving will tend to remain so unless approached closely.
 2. Snakes should never be grasped by the head, just behind the head, or by the tail. Snakes held in these locations are extremely likely to injure themselves. The best position to grasp a snake is about 1/3 of the body length behind the head.
 3. Professional snake tongs are the best tool to handle snakes. Lightweight aluminum "garbage grabbers" are not sturdy enough to handle heavy snakes, and may result in injury.
 4. Each park vehicle, the housing area, and maintenance headquarters should be equipped with one pair of snake tongs or a snake stick. The visitor center should have at least two pairs of snake tongs and snake-holding buckets.
 5. Snake-holding buckets and/or cages should have clear Plexiglas lids, adequate ventilation, a locking mechanism, and should be cleaned between captures with a disinfectant or weak bleach solution to prevent spread of diseases among snakes.

II. Nuisance Rattlesnakes

- A. Rattlesnakes found away from human use areas are not likely to impact human safety and should not be handled.
- B. Snakes of all species found crossing roads or on the edge of roads should be moved at least 20 meters (about 20 yards) off the road in the likely direction of their original travel (if moved in the opposite direction, snakes will attempt to cross the road again).
- C. Rattlesnakes found in locations where they may pose an immediate or future threat to human safety should be moved less than 50 meters from their capture point into adjacent native vegetation that provides adequate cover (but see E. below).
1. Snakes found in the winter months (early November - mid February) are almost surely near winter hibernation sites and should not be moved more than 50 m under any circumstances, as they are likely to succumb to exposure if they are not able to return to their shelter site before nightfall.
 2. Snakes found in the visitor center and housing areas in the spring or fall and are likely to be migrating to or from cliffs behind the visitor center and trails. They should be moved away from the cliffs in the spring (toward Wet Beaver Creek) and toward the cliffs in the fall.
 3. If rattlesnakes are found on visitor trails in the late spring or summer months and there are large numbers of visitors in the area, or visitors that may attempt to harass the snakes once released, they may be held until after the park closes, and re-released at their capture point. Holding snakes is not recommended in the early spring and fall months, because evening temperatures may be too cold to allow the snakes to find adequate shelter.
 4. No snake should be moved more than one kilometer (less than one mile) from its capture point, to prevent disorientation and wandering.

- D. If herpetologists are working at the park, record the capture location of each snake, and hold all rattlesnakes for processing and marking.

E. If rattlesnakes are a repeat safety issue in a particular area, identify individual rattlesnakes by painting (no more than half of any rattle segment should be colored) with an individual color combination:

1. If there is one snake repeatedly causing a serious safety issue (i.e., a snake frequenting a restroom area), that individual may be moved no more than 2 kilometers (1.25 miles) to a protected habitat that is as similar as possible to native vegetation contained near or at the capture point. The release site should not be near paved roads or heavily-used dirt roads, as these are major sources of mortality for snakes. If possible, the habitat should contain suitable hibernation sites (i.e., south-facing rock outcrops).
2. If there is more than one snake repeatedly causing a serious safety issue, the reasons for snake presence must be ascertained (see below). Removing a few snakes from such an area may not solve the long-term issue.

III. Long-Term Management Strategies

A. To decrease nuisance rattlesnake encounters in human use areas during their foraging period:

1. Focus on making human use areas less attractive to rodents by discouraging hand-feeding and bird feeding/watering, removing garbage frequently, making compost areas rodent-proof, removing brush and wood piles, and rodent-proofing buildings as much as possible.
2. To make these areas less attractive to rattlesnake prey in general, remove areas of non-native vegetation, especially lawn grasses, and discontinue frequent watering of established areas of native vegetation.
3. Fence snakes and other small animals out of yards and other small areas by properly installing and maintaining snake-proof walls around these areas, making sure that snakes are not excluded from hibernation sites.
4. (a suggestion; not tested): Consider building elevated boardwalks in areas of high rattlesnake and human use. The theory is that snakes will not like to use the exposed walkways, but will instead pass mostly unseen under them. This idea might be particularly effective in snake migratory paths.

B. For long-term conservation of park rattlesnake populations:

1. Focus on educating visitors about rattlesnake natural history, importance in the ecosystem as predators and prey, and snakebite facts, using trailside displays, roadside signs reminding people to watch for snakes, interpretive programs, brochures, and/or in-school programs.
2. Maintain existing trailside display about rattlesnakes and make sure that adequate numbers of brochures and other handouts about rattlesnakes and research at the monument are easily accessible to park staff at all times.
3. Install and maintain snake-proof walls or fencing around sewage ponds, or check these ponds on a daily basis, to prevent entrapment of snakes.
4. Maintain and keep clear existing road culverts, as snakes use these to cross under roadways.
5. Any future maintenance work in the cliff areas behind the visitor center should take into consideration the importance of these areas to snakes as hibernation sites.

