MANAGEMENT OF "NUISANCE" VIPERS: EFFECTS OF TRANSLOCATION ON WESTERN DIAMOND-BACKED RATTLESNAKES (*CROTALUS ATROX*)

Erika M. Nowak[1], Trevor Hare[2], and Jude McNally[3]

Abstract: Translocation of "nuisance" rattlesnakes from public and residential areas to undeveloped habitats is an increasingly common management practice in the southwestern United States. There are, however, concerns whether translocated animals adjust to or even survive such interventions. We independently conducted radiotelemetry research to evaluate the effects of nuisance rattlesnake translocation at two separate locations in Arizona, from 1994 to 1997. In north-central Arizona, at Montezuma Castle National Monument (MOCA), one of us (EMN) studied 19 telemetered Western Diamond-backed Rattlesnakes (*Crotalus atrox*), and compared the effects of experimental translocation of seven of these snakes translocated 2 km from the MOCA visitor center with seven controls (non-translocated). In southern Arizona, in the Tucson Rural Metro Fire District, two of us (TH, JM) studied 97 individually marked rattlesnakes, seven that were telemetered *C. atrox*. Due to a variety of constraints in the latter study, only descriptive data on post-translocation effects are provided. Although the study designs and sites were different, our results are complementary. In both studies, we found that most snakes moved greater distances and more frequently after translocation, resulting in increased activity range sizes. At the protected MOCA site, there were few statistically significant negative effects of translocation, and > 50% of the rattlesnakes returned to locations from which they were displaced. Nonetheless, the survival rate of translocated rattlesnakes was low. At the highly urbanized Tucson site, there were few recaptures of translocated snakes and mortality was high. Our research has important implications both for management of rattlesnakes in public areas and for development of more effective long-term policies for mutually safe cohabitation of rattlesnakes and humans.

Introduction

The management of "nuisance" wildlife species (those found in areas where they are not wanted by humans because they are, or are perceived as, potentially dangerous or destructive) is a ubiquitous wildlife management problem. Although lethal methods are used to manage many species (e.g., Brammer et al., 1994; Rodda et al., 1999), this approach is not always desirable or ecologically sound. Translocation of problem animals from areas where they conflict with humans is a standard, non-lethal procedure used to manage a variety of species in the United States, including Grizzly Bear (*Ursus arctos*; Blanchard and Knight, 1995), Gray Wolf (*Canis lupus*; Shirley Hoff, U. S. Fish and Wildlife Service, pers. comm.), White-tailed Deer (*Odocoileus virginianus*; Jones et al., 1997), Raccoon (*Procyon lotor*; Mosillo et al., 1999), California Ground Squirrel (*Spermophilus beecheyi*; Van Vuren et al., 1997), and rattlesnakes (*Crotalus* spp.; Perry-Richardson and Ivanyi, 1992; Hare and McNally, 1997; Moorbeck, 1998; Nowak, 1998). Translocation is a commonly practiced conservation technique in public and residential areas, particularly where concentrated and relatively wealthy human populations are encroaching into formerly natural habitats (Rideout, 1993; Brammer et al., 1994; Briggs et al., 1996). In southwestern deserts, this pattern is increasing, and the effects of habitat loss are exacerbated when wildlife is attracted to artificial oases with increased availability of food and water (Hardy and Greene, 1999a). Translocation of the resulting nuisance animals is perceived as a humanitarian solution for dealing with the problem.

Rattlesnakes are considered nuisance species and are commonly managed by translocation programs on public and private lands. Public areas, such as national parks, often must manage for visitor enjoyment and safety while at the same time protecting wildlife populations. The 1916 Organic Act states in part, "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, 1980). For this reason, translocation of rattlesnakes from visitor use areas is an especially popular, though largely ad hoc, management technique. In a 1994 survey of 26 such areas in the southwestern United States, Nowak (1998) found that parks commonly translocated nuisance rattlesnakes distances varying from several meters to 40 km. This same strategy is carried out on private lands. For example, in Pima County, Arizona, private and public fire departments and animal control agencies participated in the translocation of over

[1]USGS Southwestern Biological Science Center, Colorado Plateau Field Station, Box 5614, Northern Arizona University, Flagstaff, Arizona 86011, USA. E-mail: erika.nowak@nau.edu

[2]2718 East Croyden Street, Tucson, Arizona 85716, USA

[3]Arizona Poison Center, Arizona Health Sciences Center, 1501 North Campbell Avenue, Tucson, Arizona 85724, USA

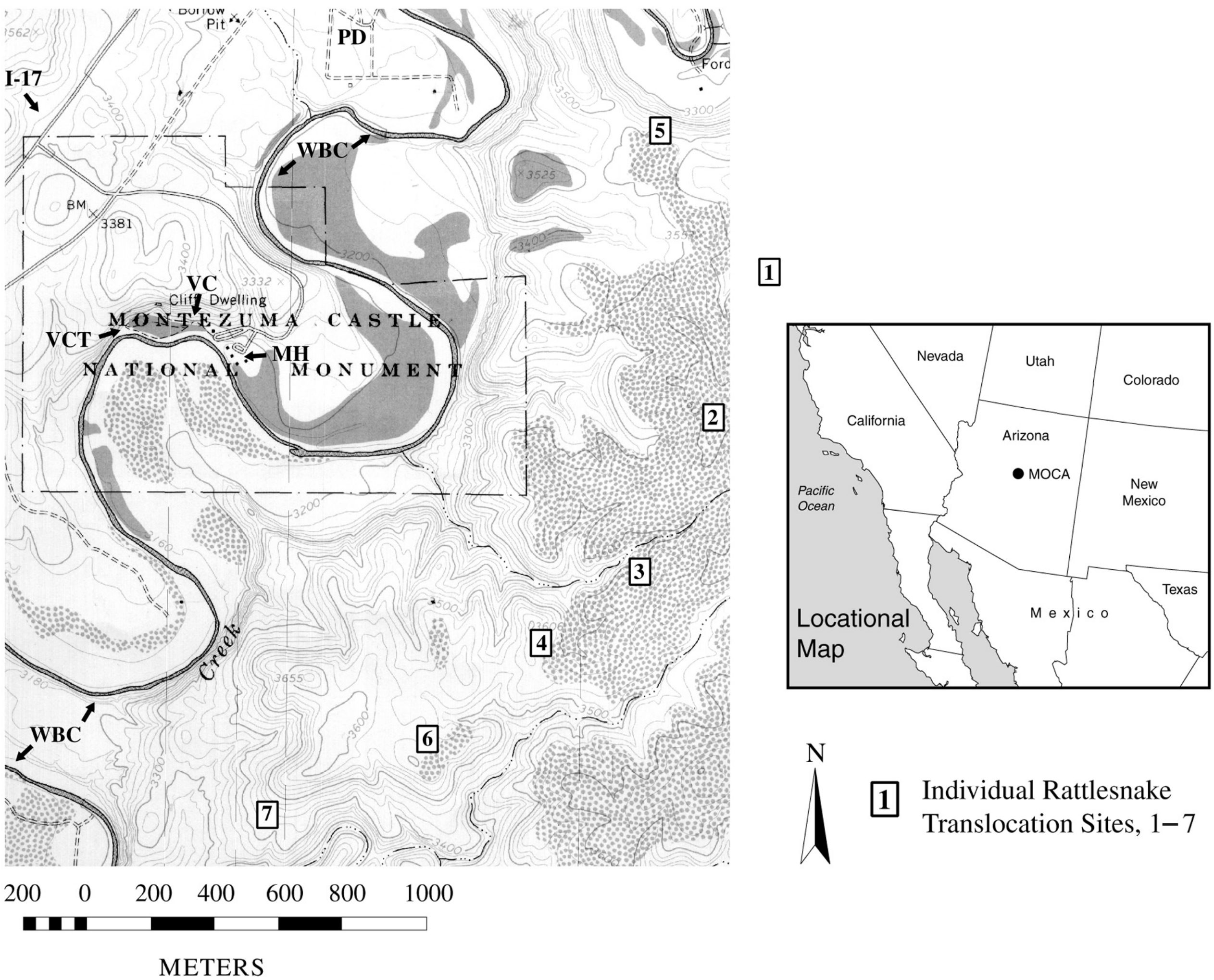

Fig. 1. Montezuma Castle National Monument (MOCA) study site for translocation research on *Crotalus atrox* from August 1994 to December 1996.

11,500 nuisance reptiles in 1997 and 1998 (G. Good, pers. comm.). These animals were usually released in large groups at distances far exceeding normal home-range areas for these species, sometimes after traveling in hot emergency response vehicles or being held for hours in fire station bays. Translocation distances and release locations are generally not based on scientific comparison of various translocation distances, but on convenience and differing human attitudes about the inherent hazard posed by rattlesnakes.

Although there is little question that removing potentially dangerous animals from an area of contact will mitigate the immediate threat to humans, this practice is not a proven conservation strategy. As human encroachment on natural wildlife habitats continues, translocation of nuisance species to more remote areas may no longer be practical or economically feasible. Additionally, the resulting effects on translocated animals have not been taken into consideration. Previous studies of translocation have shown that displaced vertebrates frequently exhibit increased mortality rates, random movements (e.g., wandering), and aberrant social behavior (Dodd and Seigel, 1991; Bright and Morris, 1994; Hambler, 1994; Lloyd and Powlesland, 1994; Compton et al., 1995; Macmillan, 1995; Sealy, 1997). Translocated rattlesnakes commonly experience increased mortality due to increased predation and/or inability to find suitable hibernation sites (Reinert and Rupert, 1999; R. Johnson, unpublished). They also exhibit aberrant movements and social behavior (Fitch and Shirer, 1971; Landreth, 1973; Galligan and Dunson, 1979; D. Virchow, pers. comm.).

To date no studies have been published on the effects of translocation on southwestern US rattlesnakes, and only one study has attempted to quantify these effects in a national park setting (R. Manasek, pers. comm.). Montezuma Castle National Monument

(MOCA) in north-central Arizona, receives approximately 900,000 visitors and has about 12 sightings of Western Diamond-backed Rattlesnakes (*Crotalus atrox*) and Northern Black-tailed Rattlesnakes (*Crotalus m. molossus*) each year (S. Sandell, pers. comm.). Prior to 1994, at least 75% of the nuisance rattlesnakes were removed from the monument to adjacent National Forest Service land.

The Tucson Rural Metro Fire Department (RMFD) serves unincorporated areas of Pima County in southern Arizona, and routinely translocates nuisance reptiles [including five species of rattlesnakes, Arizona Coralsnakes (*Micruroides e. euryxanthus*), Gila Monsters (*Heloderma suspectum*), and at least 10 species of non-venomous snakes] at the request of department subscribers. In 1992, firefighters in the RMFD concerned with the increasing numbers of reptiles being translocated, contacted two of us (TH and JM) at the Arizona Poison and Drug Information Center to encourage research into this issue. In 1993, we (TH and JM) documented the translocation of over 200 snakes from one fire department station within the RMFD in the Catalina Foothills.

From 1994 to 1997, we independently conducted experimental translocation studies on rattlesnakes: one study at MOCA (Nowak, 1998), and one at the urban/desert interface within the RMFD (Hare and McNally, 1997). In this paper we detail the results of our two separate studies. After comparing results, we discuss the effects of translocation on movement patterns, survival, behavior, and potential disease transmission of *C. atrox* at our two study sites, and suggest management strategies for the conservation of venomous snakes in both public and residential contexts.

MONTEZUMA CASTLE NATIONAL MONUMENT

MATERIALS AND METHODS

Study Site

Montezuma Castle National Monument is located in the Verde Valley of north-central Arizona, at ca. 1,158 m elevation (Fig. 1). The 235 ha Castle Unit of the monument is bordered to the north, east, and south by United States Forest Service property (Beaver Creek Ranger District), and to the west by an Interstate highway (I-17). The monument 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 Creosote-Crucifixion-thorn Series of the Arizona Upland Division of the Sonoran Desertscrub, but vegetation representative of the Chihuahuan, Mojave, and Great Basin desertscrubs are also present (Turner and Brown, 1994). Porous limestone outcroppings and cliffs are prominent landscape features.

Capture Methods

From June 1994 to December 1996, 28 *C. atrox* were captured at MOCA. All were restrained in plastic tubes, measured (snout-vent length, tail length, and body mass), and sexed by probing. All were individually marked with paint on the distal half of the basal three rattle segments (the whole rattle was not painted to deter detection from aerial predators while the snakes were at rest) with individual color combinations using semi-permanent Testor's model paint, and released within 10 m of their capture sites. Ten adult male and nine non-pregnant females were held for radiotransmitter implantation. Snakes were measured for snout-vent-length (SVL) and body mass ($\bar{x} \pm$ SD). Mean male size was 106 ± 18 cm SVL (range 78–140 cm) and 878 ± 409 g (range 334–1,681 g). Mean female size was 91 ± 11 cm SVL (range 76–102 cm), and 448 ± 117 g (range 268–604 g).

Telemetry Methods

We used temperature-sensing implantable radiotransmitters from Telonics Telemetry-Electronics Consultants (Mesa, Arizona) and Holohil Systems, Ltd. (Ontario, Canada). Transmitters ranged from 11.0 to 13.8 g, and battery life was ca. 12 months for Telonics, and 24 months for Holohil. Each transmitter was less than 5% of body mass of the snake.

Snakes were anesthetized at a veterinary hospital in a retrofitted aquarium using Isoflurane vapor. Anesthesia was administered by tracheal entubation during surgery, and the lungs were artificially inflated during and after surgery to ensure adequate anesthesia and oxygenation. Veterinarians used sterile surgical procedures to implant a radiotransmitter in the coelomic cavity of each rattlesnake, in the posterior third of the body anterior to the vent, following typical implantation procedures developed for snakes (Reinert 1992; Hardy and Greene, 1999b). Several animals with previously acquired wounds or infections were given a single, small dose of the antibiotoc Amikacin®. All subjects were held in a heated room and provided with water ad libitum for at least 12 h to ensure adequate recovery from anesthesia. One snake died during surgery.

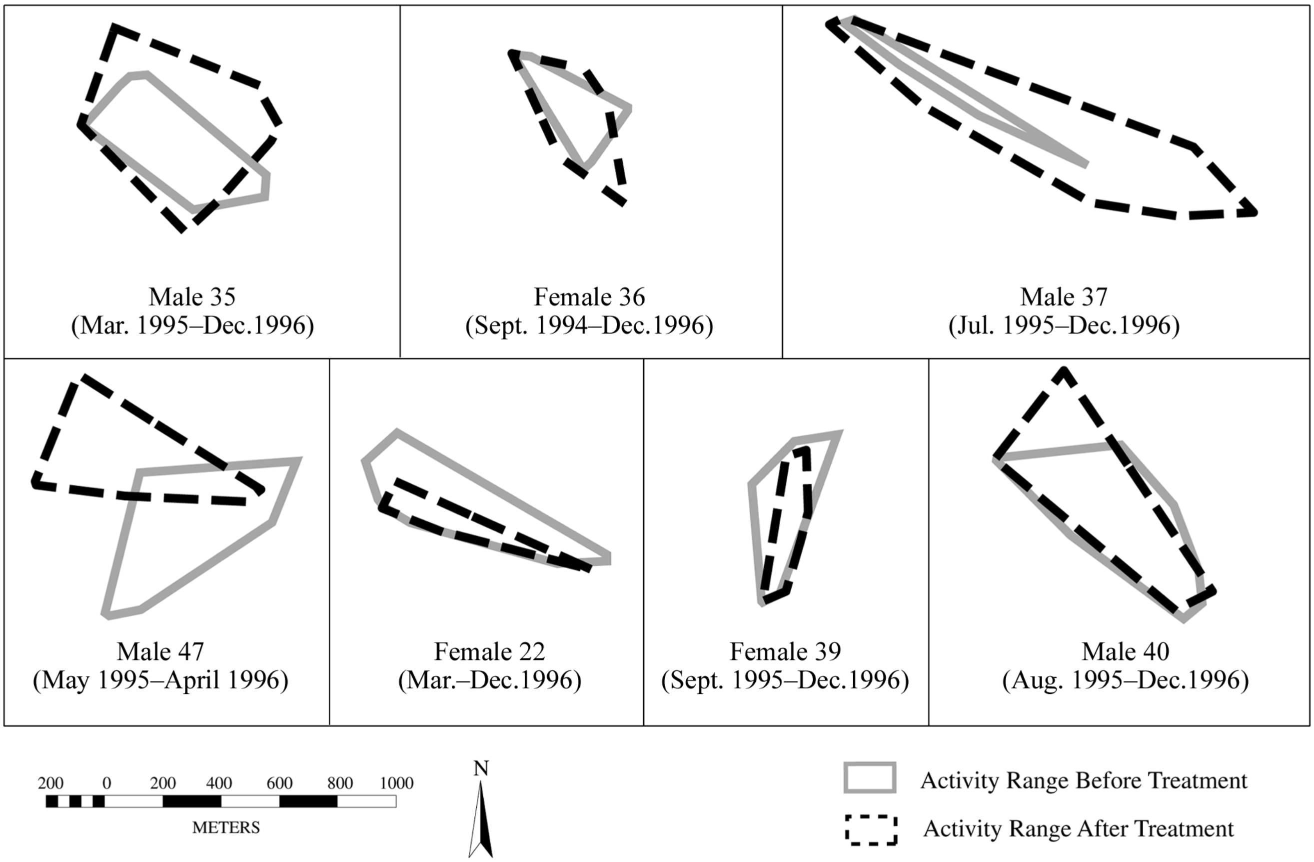

Fig. 2. Activity ranges (estimated by the minimum convex polygon method) for seven control *C. atrox* before and after handling treatment at MOCA from August 1994 to December 1996.

We returned all snakes to their original area of capture after recovery from transmitter implantation, and recorded their position every second day during their active period (generally mid-March to mid-October) from August 1994 to December 1996. Two males and one female were tracked every day from August to October 1994, and their between-day movements were small (E. Nowak, unpublished). Given this finding, as well as funding and time constraints, we decided to locate the snakes every two to three days. We located all rattlesnakes every two weeks during hibernation. The 19 subjects were located a total of 1,648 times. Mean number of locations per snake was 87 ± 49, range 5–187). We recaptured, weighed, and measured implanted snakes just after egress from hibernation, once during mid-summer, and just prior to hibernation to assess condition and growth. Additionally, four snakes had to be recaptured to implant new transmitters.

We used a Trimble Navigation (Sunnyvale, California) Geo-Explorer Global Positioning System Unit (GPS) to record positions of the snakes in Universal Transverse Mercators (UTM) values. All GPS locations were corrected to within 3 m accuracy with the USGS Colorado Plateau Field Station Base Station using Trimble Pathfinder software. Snake locations, movement patterns, and activity range polygons were mapped using ESRI ARC/Info (Redlands, California).

Translocation

Fourteen *C. atrox* were translocated at MOCA. One male and four females could not be located after several months due to transmitter failure. These were considered non-experimental animals, and their data are not included (see Nowak, 1998). Translocation occurred only after all snakes had been tracked for at least two weeks. Over a two-day period in mid August 1995, three males and one female were selected at random (after stratifying by sex), placed in separate opaque 19-liter buckets, and hand-carried to separate translocation sites 2 km east of the MOCA visitor

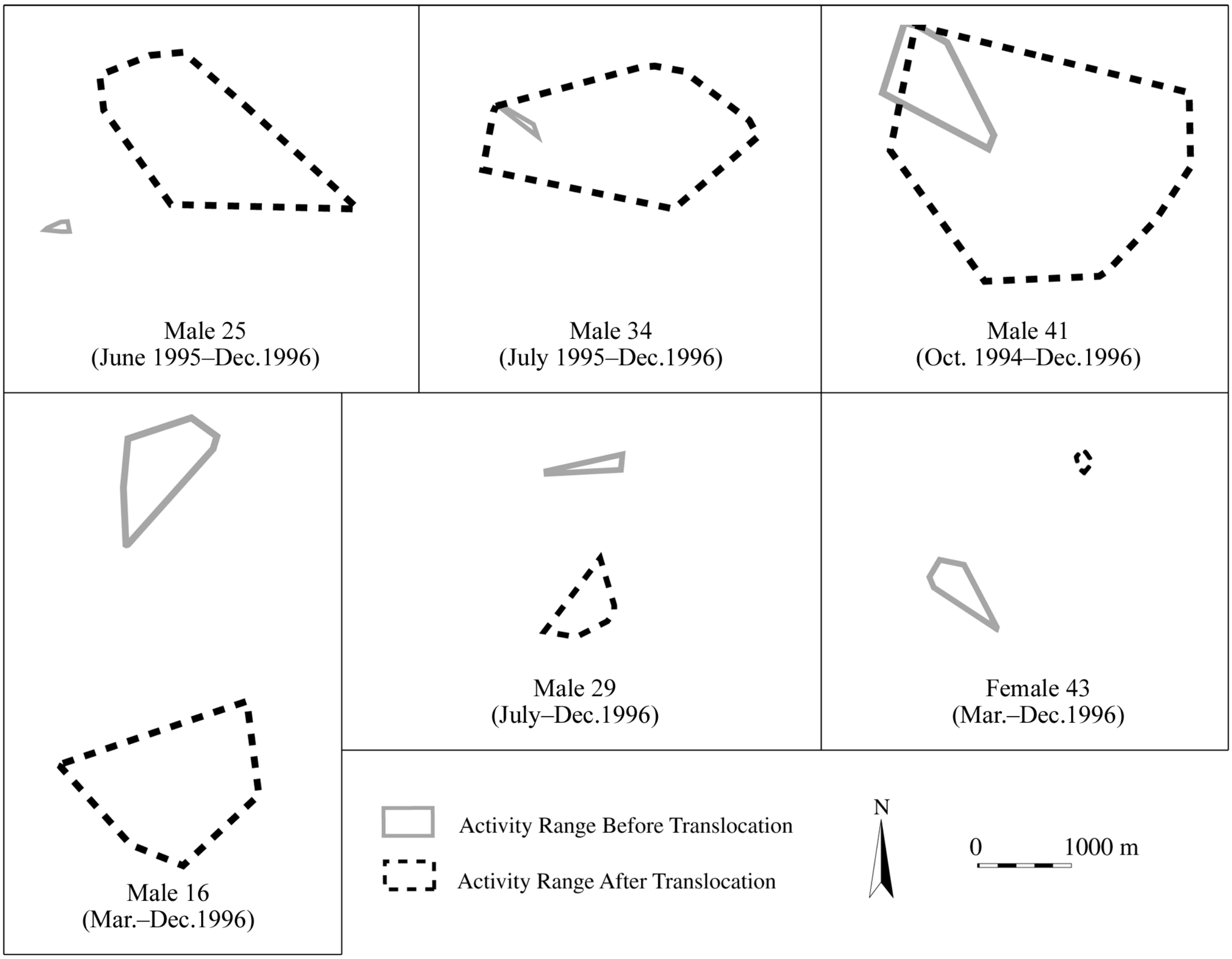

Fig. 3. Activity ranges (estimated by the minimum convex polygon method) for six translocated *C. atrox* before and after translocation at MOCA from August 1994 to December 1996.

center on US Forest Service property (Fig. 1). This translocation distance was twice the value any snake was known to move in a straight-line distance during one active season, and we thus define it as long-distance translocation (LDT). Other authors (e.g., Hardy and Greene, 1999a), however, define this distance as within the range of short-distance translocation (SDT). Translocation sites were chosen using a stratified random sampling procedure to place the snakes at least 0.5 km apart from each other in habitat contiguous with the monument that did not contain developed communities, roads, and/or heavily-used recreation areas. At the same time, three males and one female were placed in opaque buckets, carried a distance equivalent to 2 km, and re-released at their latest capture points at MOCA. These non-translocated snakes provided a control for any effect of handling of the translocated snakes, and are henceforth referred to as "control" snakes. We repeated this experiment in mid August 1996, with six *C. atrox* not previously involved in the experiment: one female and two males were translocated, and one female and two males were used as controls.

Data Analyses and Presentation

We determined the effects of translocation by comparing within treatment groups (i.e., control or translocated snakes) before and after the translocation 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, and season. Translocated snakes were excluded from the second type of analysis. For all parametric data analyses we log-transformed non-normally distributed data, and verified homogeneity of variance using Levene's test (Neter et al., 1990). Significance was set at $P \leq 0.05$. Means are reported as ± one standard deviation (SD).

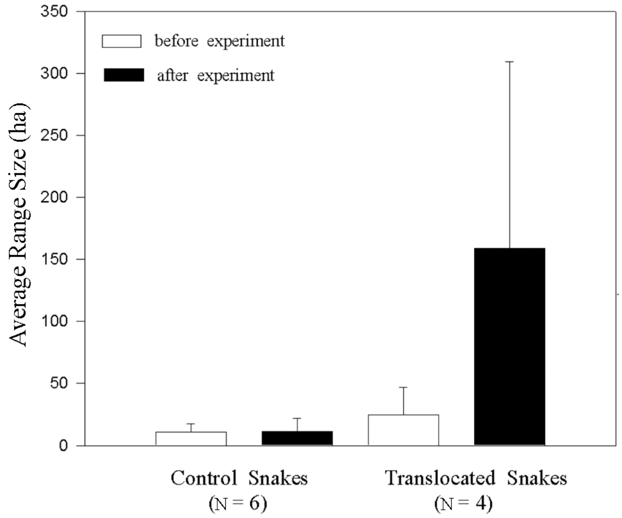

Fig. 4. Average activity range sizes (estimated in hectares by the minimum convex polygon method) for six control compared to four translocated *C. atrox* before and after a translocation experiment at MOCA from August 1994 to December 1996.

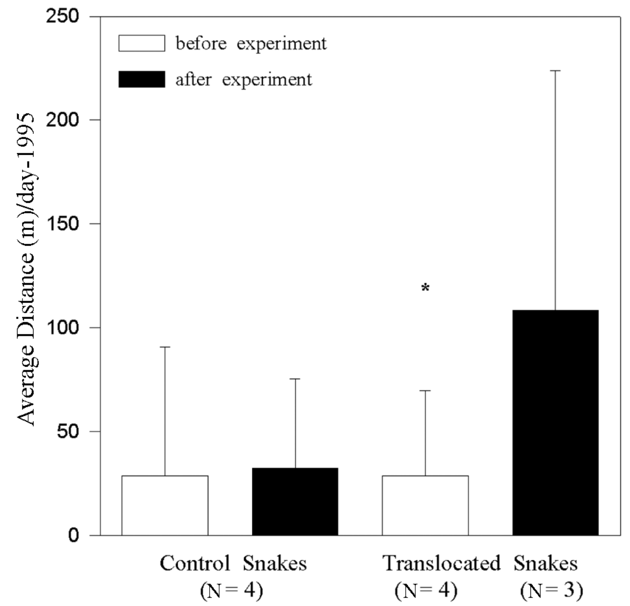

Fig. 5. Average distance (in meters) moved per day during the 1995 active season for control and translocated *C. atrox* before and after a translocation experiment at MOCA from March 1995 to November 1995. * = significance at the $P \leq 0.05$ level ($t = 7.76$; $df = 2$; $P = 0.02$).

Activity Range Analyses

We used the minimum convex polygon method (White and Garrott, 1990) in the program Telem (K. McKelvey, pers. comm.) to estimate activity range for each snake. Because the size of the activity range of any animal is largely dependent on the number of locations (Reinert, 1992), the data were standardized. To compare activity range sizes between the translocated 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. This time period was derived from a time-series analysis of activity range size in which it was determined that many non-translocated snake range sizes reached an initial plateau at about eight weeks (E. Nowak, unpublished). To compare the activity range of each snake before and after treatment, we standardized the data for each snake by comparing the shortest number of weeks immediately preceding or following the experiment (e.g., when a snake was tracked for eight weeks before the experiment and 20 weeks after, we compared the eight weeks before only with the eight weeks immediately after the experiment).

Movement Pattern Analyses

To determine if there were changes in movement patterns of the snakes resulting from the translocation experiment, the following indices were calculated: (1) average distance (in meters) moved per day; (2) frequency of movement between consecutive locations; (3) total distance traveled from the release site at the time of the experiment to the first hibernation location used; and (4) 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 6 m 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 and June, prior to summer rains), wet summer (July and September, during summer rains), and fall (September and October).

Average distance moved per day was calculated by dividing the distance between successive locations by the number of days between successive locations for the active season. 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.

We analyzed directionality of movements between successive locations for the four treatment groups and

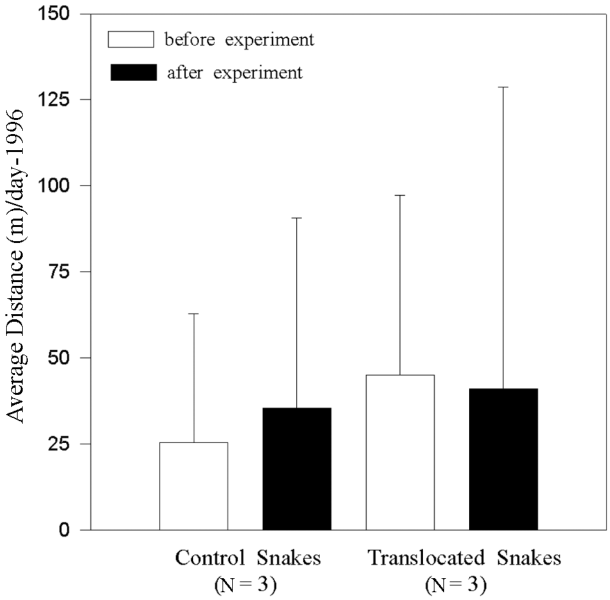

Fig. 6. Average distance (in meters) moved per day during the 1996 active season for control and translocated *C. atrox* before and after a translocation experiment at MOCA from March 1996 to November 1996.

that of individual snakes, to determine if individuals exhibited different patterns, in both the first few months after treatment and in the second year after treatment using the Watson's U^2_n-test for randomness (Batschelet, 1981). Directionality was further analyzed by dividing data for individual snakes into movements between consecutive locations between six and 99 m, and ≥ 100 m. 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 Analyses

To assess changes in condition of the rattlesnakes we calculated growth rates for each snake by determining total change in SVL. The relative importance of experimental and extra-experimental effects on the regression of the natural log-transformed body mass (log-mass) to SVL was determined using MANOVA tests (Neter et al., 1990). We used residuals of log-mass to SVL as an index of condition and compared translocated vs control groups. Changes in the condition of individuals over the entire study were determined by averaging the change in mass for each snake during the periods before and after treatment.

RESULTS

The foraging and hibernation ecology of the MOCA population of *C. atrox* and other movement parameters (including movements during hibernation and the number of new locations used) are discussed in detail elsewhere (Nowak, 1998).

Activity range size.—The activity range sizes did not differ significantly before and after handling during equivalent time periods ($t = 0.02$, $df = 6$, $P = 0.98$). The average range size for the translocated group was 24.27 ± 22.16 ha before translocation and 59.58 ± 57.22 ha after translocation during equivalent time periods (Fig. 3). Four of six translocated rattlesnakes had activity range sizes that increased greatly after treatment, and two had activity ranges that decreased when compared to those prior to translocation. Due to individual variation, however, the trend of increasing post-translocation range size was not statistically significant ($t = -1.15$, $df = 5$, $P = 0.30$).

When the translocated and control groups (Fig. 2) 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 translocated snakes before the experiment ($t = -0.44$, $df = 8$, $P = 0.67$). Although there was a trend for translocated snakes to have larger activity ranges than controls after translocation, it was not significant ($t = -1.56$, $df = 8$, $P = 0.16$; Fig. 4).

We did not detect any significant extra-experimental impacts on the average activity range size of non-translocated rattlesnakes at MOCA. There was no impact of study year on the ranges ($t = -1.82$, $df = 19$, $P = 0.09$). 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 larger activity ranges, there was no statistically significant impact of sex ($t = 0.62$, $df = 13$, $P = 0.55$). The average activity range for males was 19.03 ± 16.01 ha and 8.48 ± 3.87 ha, for females. The variation in range size, however, was significantly higher for males than for females ($F = 13.45$, $P = 0.002$).

Movement patterns: *average distance moved per day*.—A thorough description of changes in movement patterns following translocation of MOCA rattlesnakes may be found in Nowak (1998). One translocated female rattlesnake at MOCA moved more than 1 km in the first two days after translocation in 1995, then disappeared and was not located again during the study, even during aerial tracking attempts in the area.

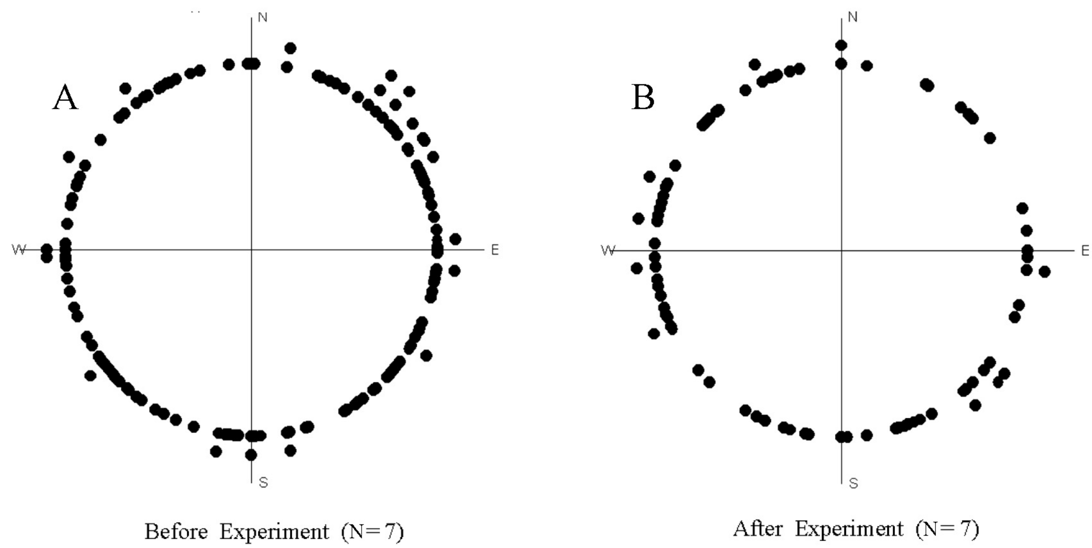

Fig. 7. Direction of movement between consecutive locations for control *C. atrox* at MOCA during a translocation experiment from August 1994 to December 1996. (A) Movements before handling experiment. (B) Movements after experiment..

In 1995, there was no significant difference in average distance moved per day during the active season for the control snakes before and after the experiment ($t = -0.79$, $df = 3$, $P = 0.49$), but there was a significant difference for translocated snakes before and after the experiment ($t = 7.76$, $df = 2$, $P = 0.02$) (Fig. 5). In the between-group comparisons, the control and translocated snakes did not differ significantly in distance moved per day before the experiment ($t = -0.84$; $df = 129$; $P = 0.40$) but did differ after the experiment ($t = -3.27$; $df = 72$; $P = 0.002$). In 1996, there was no significant difference in average distance moved per day for the control snakes before and after the experiment ($t = 2.86$, $df = 2$, $P = 0.10$), and there was no significant difference for translocated snakes before and after treatment ($t = -0.26$, $df = 2$, $P = 0.82$) (Fig. 6). In the between-group comparisons for 1996 data, control and translocated snakes did not significantly differ in average distance moved per day before ($t = -0.82$, $df = 78$, $P = 0.07$) or after the experiment ($t = 0.33$, $df = 29$, $P = 0.74$). These conflicting results between years are likely due to small sample sizes (only three snakes in each group) and to individual variation. Even climatic differences between years are a possible influence to consider.

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 for MOCA rattlesnakes (Nowak, 1998). When the average distance moved per day was compared between males and females, there was a non-significant trend for males to move a greater distance per day than females. In 1995, males moved 50.85 ± 79.03 m/day, and females moved 30.72 ± 57.08 m/day ($t = 1.66$, $df = 208$, $P = 0.10$). In 1996, males moved 37.55 ± 45.51m/day, and females moved 31.57 ± 51.98 m/day ($t = 0.58$, $df = 163$, $P = 0.56$).

Frequency of movement.—The frequency of movement to new locations did not differ between control and translocated groups before or after the experiment ($\chi^2 = 50.50$, $df = 51$, $P = 0.49$). Within groups the frequency did not differ significantly before and after the experiment (control $Z = -1.48$, $P = 0.14$, translocated $Z = -0.53$, $P = 0.59$). The frequency of movement for controls was 0.67 ± 0.26 before and 0.79 ± 0.14 after treatment, and 0.71 ± 0.20 before and 0.82 ± 0.06 after for translocated snakes. There were no extra-experimental effects on the frequency of movement of the control snakes, and no difference in the actual number of new locations used between or within treatment groups (Nowak, 1998).

Distance traveled after release.—No significant difference was found in the distance moved by the control snakes between the experimental release site and the first hibernation site used ($t = 1.98$, $df = 5$, $P = 0.10$), so these data were combined for 1995 and 1996 releases. There was no significant difference in the distance moved between release site and first hibernation site of control and translocated snakes: control snakes moved an average of 1,729.55 ± 1,040.13 m between release site and first hibernation site, and translocated snakes moved an average of

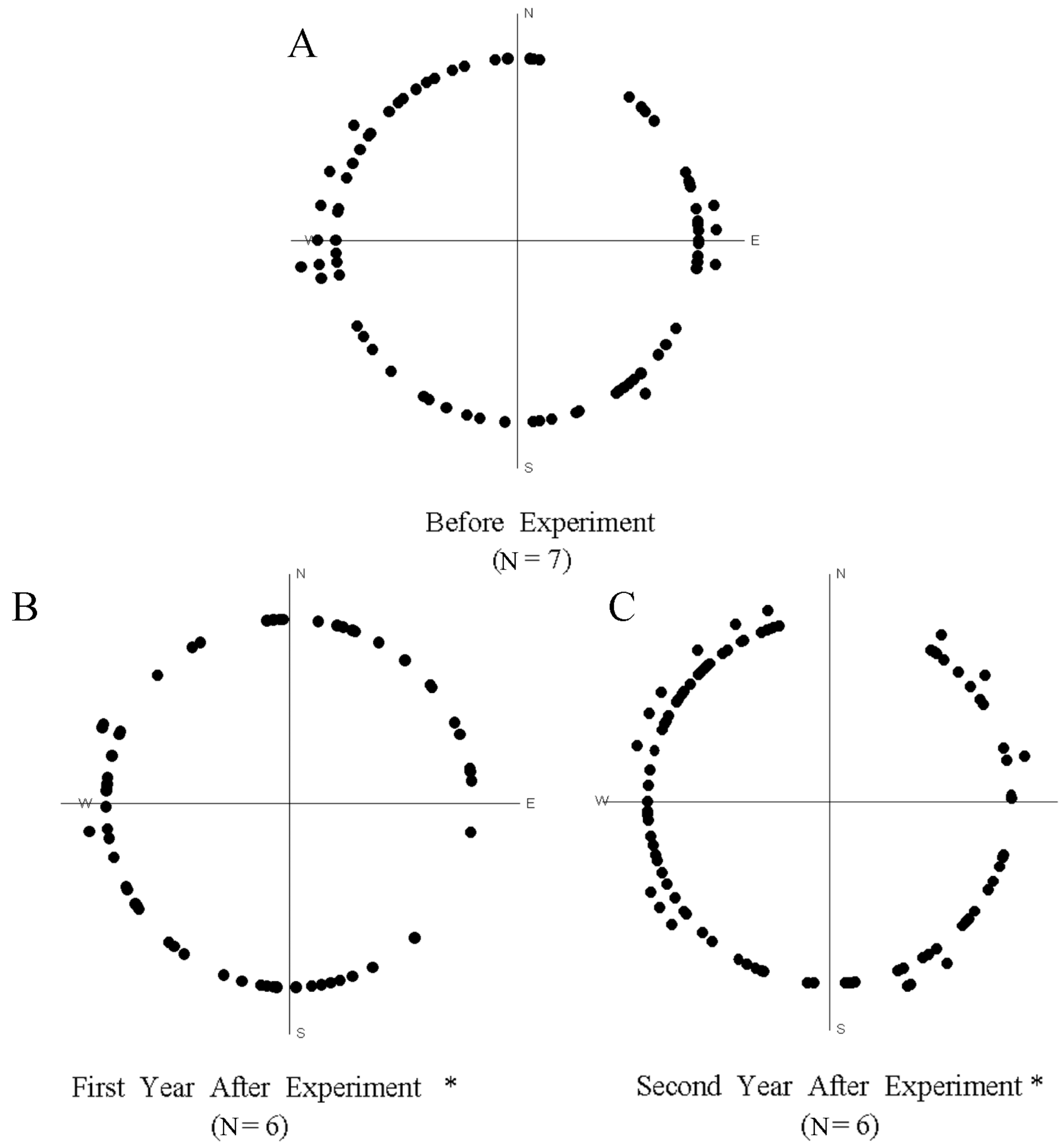

Fig. 8. Direction of movement between consecutive locations for translocated *C. atrox* at MOCA during a translocation experiment from August 1994 to December 1996. (A) Movements before experiment. (B) Movements in the first few months after experiment (U^2_n = 0.23; $P < 0.05$). (C) Movements in the second year (1996) after experiment (U^2_n = 0.20; $P < 0.05$. * = a non-random pattern of movement with significance at the $P \leq 0.05$ level.

3,677.74 ± 2,488.45 m ($t = -1.61$, $df = 11$, $P = 0.14$).

The estimated total distance moved by male 41 after translocation (i.e., between release in 1995 to final hibernation in 1996) was 15.7 km. Translocated male 34 moved 14.5 km during the same time period, and the only similar-sized control male (37) moved 9.1 km.

Directionality of consecutive movements.—The movements between consecutive locations for control snakes did not differ significantly from random before (U^2_n = 0.12, $P > 0.05$) nor after treatment (U^2_n = 0.15, $P > 0.05$) (Fig. 7). The directional movement pattern between consecutive locations for the translocated snakes did not depart significantly from random (U^2_n = 0.07, $P > 0.05$) before treatment, but was significantly non-random in the first few months after translocation (U^2_n = 0.23, $P < 0.05$) and the second year after translocation (U^2_n = 0.20, $P < 0.05$) (Fig. 8). This non-random pattern did not translate into a significant mean bearing either immediately following translocation ($R = 9.91$, $P > 0.05$) or the year following ($R = 16.57$, $P > 0.05$). Three individuals (two translocated males and one control female) had consecutive movements that departed significantly from random with significant mean bearings after treatment (Nowak, 1998).

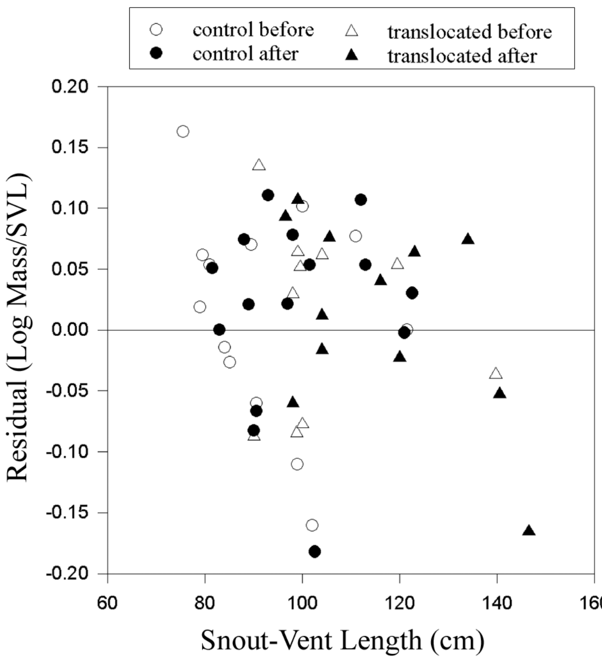

Fig. 9. Residuals of the regression of the log of mass ("log-mass," in grams) to snout-vent length ("SVL," in centimeters), vs SVL for 7 control and 6 translocated *C. atrox* before and after treatment during a translocation experiment at MOCA from August 1994 to October 1996. Each snake was measured approximately three times a year. The expected normal regression line is drawn through the Y-axis.

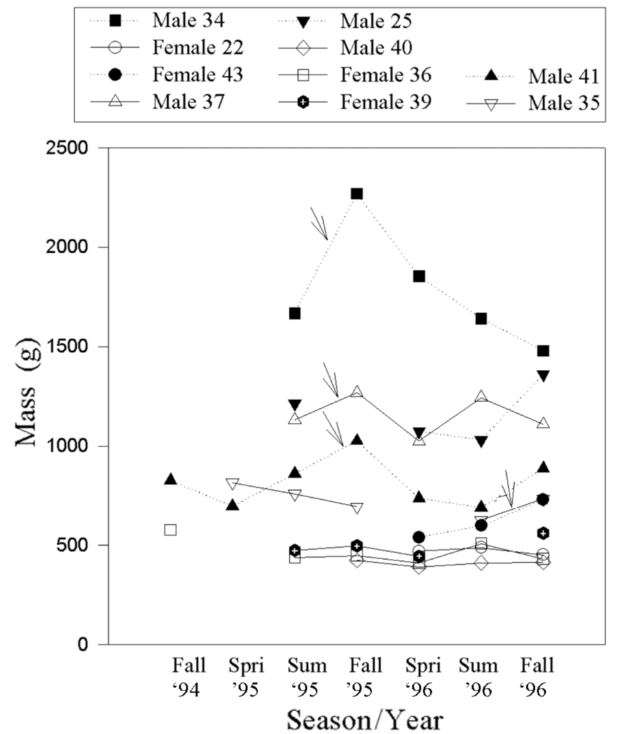

Fig. 10. Change in mass of 10 individual *C. atrox* during a translocation study at MOCA from August 1994 to October 1996. Season and year when measurements were taken are shown on the X-axis. Solid lines and open symbols represent control snakes; dotted lines with solid symbols represent translocated snakes. The time of translocation for each translocated snake is shown by an arrow.

When movements between consecutive locations were divided into lesser and greater than 100 m, and analyzed separately, there was no clear pattern. Two individuals exhibited non-random movements (Nowak, 1998). A control male (37) had non-random movements > 100 m before treatment ($U^2_n = 0.23$, not enough data to determine the significance of the mean bearing). Translocated male 34 had non-random movements from six to 99 m the second year after translocation ($U^2_n = 0.24$, $R = 7.96$; significant mean bearing of 224º, $P < 0.05$).

When the data for non-translocated snakes were analyzed by season, only during dry summer was there significant departure from random with a significant mean bearing of 110º ($U^2_n = 0.18$, $R = 19.56$, $P < 0.05$). There was no clear pattern of directional movements when seasonal effects were examined for individual non-translocated snakes (Nowak, 1998). 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, in the dry summer of 1996 there was 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 the dry summer had consecutive movements that departed significantly from random, with a significant mean bearing of 47º ($U^2_n = 0.20$, $R = 11.34$, $P < 0.05$).

Changes in condition.—We measured (SVL and body mass) two rattlesnakes in the field (unanesthetized) and at the veterinarian's office (anesthetized) less than two weeks apart. In these duplicate measurements, field measurements of SVL were slightly less (1–3%) 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 5%.

As expected, SVL and mass were strongly correlated in this population of *C. atrox* ($r^2 = 0.87$, $P = 0.0002$). Treatment did not have an effect on the relationship of the natural log of body mass (log-mass) to SVL in this population ($F = 0.184$, $df = 3$; $P = 0.91$), and interaction between the different status levels (e.g., control before treatment, translocated after treatment) was not significant ($F = 1.28$, $df = 3$, $P = 0.31$).

When residuals of log-mass to SVL (indices of health) of control vs translocated snakes were compared, there was no significant difference between the groups before treatment ($t = 0.07$, $df = 21$, $P = 0.95$) or after treatment ($t = 0.18$, $df = 25$, $P = 0.86$) (Fig. 9).

There was no significant difference in average change in mass within the control group before vs after the experiment ($t = 0.60$, $df = 5$, $P = 0.58$), or within the translocated snakes before vs after ($t = 0.05$, $df = 3$, $P = 0.96$). There was no significant difference in average change in mass before the translocation experiment between groups ($t = -0.43$, $df = 8$, $P = 0.68$) or after ($t = 0.65$, $df = 9$, $P = 0.53$).

When extra-experimental effects on the relationship of mass to SVL were examined, year of the study did not contribute significantly to the relationship model ($F = 1.65$, $df = 1$, $P = 0.21$). There was, however, a significant effect of sex of the snake on the relationship between SVL and mass ($F = 10.83$, $df = 1$, $P = 0.002$), with males significantly longer and heavier than females.

When extra-experimental effects were examined for residual indices, year of the study did not have an effect ($t = 1.69$, $df = 37$, $P = 0.10$). Residuals were significantly different between males and females ($t = 3.27$, $df = 35$, $P = 0.002$). Males had a slightly positive average residual, and females had a slightly negative residual and significantly larger variation among individuals ($F = 8.03$, $P = 0.007$).

Changes in the mass of at least four individual snakes over the course of the study showed a cyclical pattern roughly corresponding to season (Fig. 10), but there were insufficient data to determine if this effect was significant. Average change in mass of males vs females was not significantly different ($t = 0.08$, $df = 14$, $P = 0.93$), nor was there a significant difference between years ($t = -0.77$, $df = 14$, $P = 0.45$).

Mortality.—Four of seven (57%) translocated snakes died or could not be re-located, and one control snake died. Translocated female 23 could not be located two days after translocation. Mortality can neither be ruled out nor confirmed in this case. Two confirmed mortalities occurred and both were translocated animals. Male 34 steadily lost mass from fall 1995 until his death in January 1997. He was found outside his hibernaculum two to seven days after death and probably succumbed to disease or exposure. His mouth was filled with bloody, viscous fluid, suggesting a bacterial and/or viral infection at the time of death. The second mortality was female 43. Parts of her body and whole transmitter were found in the translocation area in fall 1997, but the cause and timing of death were not clear as she was last located alive and healthy three months previous. She was found < 50 m from a recently bulldozed site, but it was not evident whether this activity was involved in her death.

Two transmitters were found in 1997 for (one control and one translocated snake), suggesting either that they were expelled from the body (e.g., out the incision wound) or mortality occurred (Nowak, 1998). Mortality through natural predation is more likely, as they were found with obvious bite marks and punctures. Interestingly, the transmitter of translocated male 41 was last found in the yard of a private residence ca. 1 km northeast of the monument in an area the snake had never been located during three years of tracking.

Homing abilities after translocation.—Two of four rattlesnakes translocated in 1995, both males, returned to the monument in 1996 (Nowak, 1998). While both wandered extensively within the translocation area, they eventually made fast, parallel movements (apparent straight-lines) from the translocation area to MOCA (Fig. 11). The activity range of each snake prior to and after translocation overlapped extensively. As an example, Figure 12 illustrates the comparative ranges of male 41. Each snake was located several times in the same refugia and hibernacula that they used prior to translocation. Two of three rattlesnakes translocated in 1996 (both males) returned to the monument in 1997. Locations were not collected regularly for rattlesnakes in 1997, so the exact route followed by the snakes on their return to the monument and their respective dates of arrival are unknown.

DISCUSSION

Effects on control snakes.—Activity range sizes, movement patterns, behavior, and condition of the MOCA control rattlesnakes did not appear to be affected by handling or being carried in buckets. This result is consistent with other studies of telemetered free-ranging rattlesnakes (Reinert, 1992; Reinert and Rupert, 1999). The finding that handling does not appear to affect control rattlesnakes adds validity to any comparisons of translocated snakes from MOCA with those of the Tucson study.

Changes in activity range size.—Generally, southwestern US rattlesnakes do not have large foraging or activity ranges, and usually not dispersing more than 4 km in a straight-line from their hibernacula during the foraging season (Gannon and Secoy, 1985; King

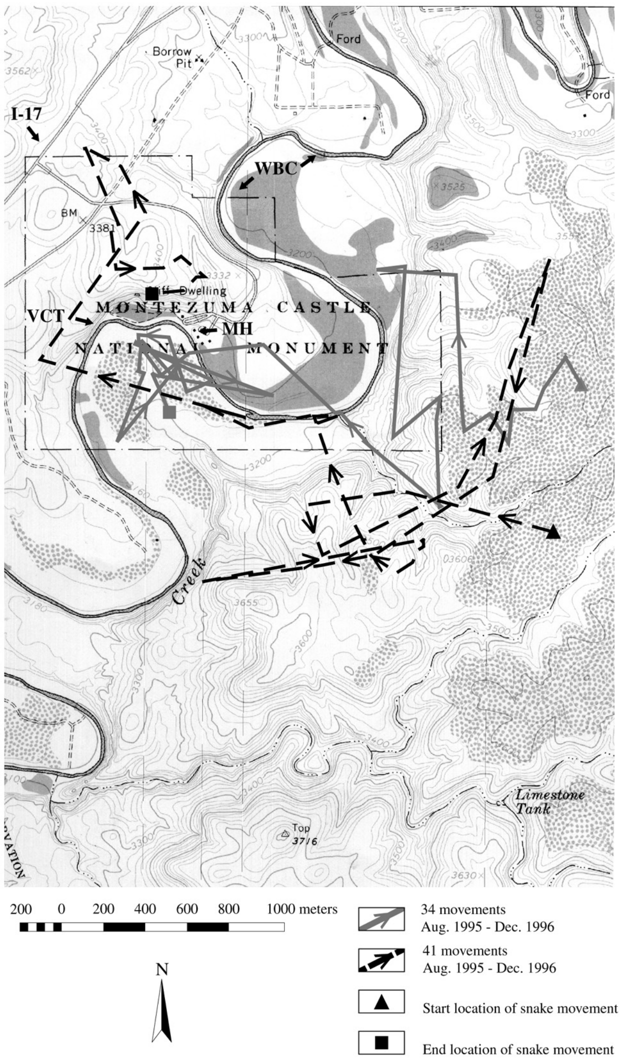

Fig. 11. Movement pattern between successive locations for *Crotalus atrox* (males 34 and 41) after experimental translocation at MOCA in August 1995.

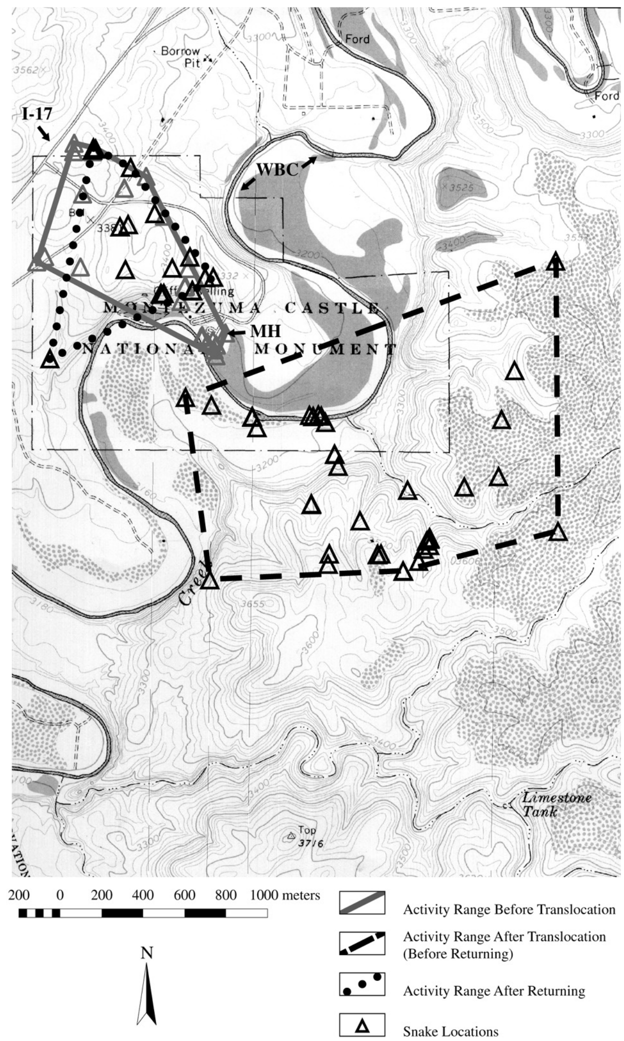

Figure 12. Activity range and locations for *Crotalus atrox* (male 41) after experimental translocation at MOCA in August 1995.

and Duvall, 1990). We found that non-translocated *C. atrox* at MOCA had activity ranges that averaged 30 ha. This is larger than the average of 5.4 ha noted for *C. atrox* in southern Arizona by Beck (1995).

More than 50% of the *C. atrox* increased their range sizes after translocation. This response is typical of many translocated animals, both in the first few months after translocation and in the subsequent year. It may be attributable to the search for prey and/or refugia in unfamiliar and structurally dissimilar habitats, increased inter- and/or intra-specific competition for space and resources, or attempts at homing. Increased activity range sizes have also been observed in translocated White-tailed Deer (Jones et al., 1997), California Ground Squirrels (Van Vuren et al., 1997), Common Dormice (*Muscardinus avellanarius*; Bright and Morris, 1994), and Bullsnakes (*Pituophis melanoleucus* [= *P. catenifer sayi*]; Moriarty and Linck, 1995). Translocated male Timber Rattlesnakes (*Crotalus horridus*) in Pennsylvania had activity ranges that were 10 times larger than those of residents (Reinert and Rupert, 1999).

Changes in movement patterns.—Movement patterns of rattlesnakes have been studied in detail by many researchers (e.g., Macartney et al., 1988; Reinert and Zappalorti, 1988a; Duvall et al., 1990; Martin, 1992; Weatherhead and Prior, 1992; Beck, 1995; May et al., 1996; Duvall and Schuett, 1997; Reinert and Rupert, 1999). Based on these studies, the maximum straight-line distance rattlesnakes disperse from their hibernacula is typically 4 km, but the typical distance for C. atrox in Arizona is 300 to 700 m (Beaupre, 1995; Beck, 1995). Hardy and Greene (1999a) noted straight-line movements of 1.5 km for

Northern Black-tailed Rattlesnakes (*C. m. molossus*) in southeastern Arizona. The typical movement pattern for rattlesnakes during most of the foraging season is to move long distances infrequently and make short-distance foraging movements within small patches of high concentrations of prey odor (Duvall et al., 1985).

Although we do not have sufficient data to determine actual movement rates and distances for the rattlesnake population at MOCA, trends in movement pattern indices for the translocated snakes after treatment are opposite those expected for free-ranging rattlesnakes. In 1995, translocated snakes moved greater distances per day after treatment, and greater distances per day than controls. They also tended to move a greater total distance and moved more frequently. These results are consistent with those found for translocated *C. horridus* (Reinert and Rupert, 1999), which traveled > 2.5 times farther than resident rattlesnakes. We interpret these aberrant post-translocation movements as evidence that the snakes were lost and possibly showing homing behavior (i.e. wandering). These patterns have been observed for translocated *C. atrox* (Landreth, 1973), other species of snakes (Parker and Brown, 1980; Reinert and Rupert, 1999), and, in general, other vertebrates (Bright and Morris, 1994; Compton et al., 1995; Van Vuren et al., 1997). For example, several translocated adult rattlesnakes traveled in straight-line distances away from the release point until they were lost (Fitch and Shirer, 1971; Landreth, 1973; Galligan and Dunson, 1979; D. Virchow, pers. comm.).

It is unknown why translocated snakes in this study did not move a greater distance per day in 1996. The primary explanation for this discrepancy is likely individual variation. Female 43 made few movements after translocation in 1996, and hibernated in close proximity to her release site. We had no evidence that this snake was pregnant. This behavior may be an alternative response to translocation to an unfamiliar area late in the activity season: to "sit tight" and conserve energy until the following year and then begin explorations. Abruptly smaller activity ranges immediately after translocation, however, are apparently rare as we could find no published reference to this phenomenon in the literature. One unpublished observation of this behavior was made during a translocation experiment with Prairie Rattlesnakes (*C. viridis*) at Scotts Bluff National Monument in Nebraska (D. Virchow, pers. comm.).

Directionality of movements has been studied in *C. atrox* (Landreth, 1973) and in Brown Treesnakes (*Boiga irregularis*; Santana-Bendix, 1994). Based on their and our field observations, we expected that the typical movement pattern for resident rattlesnakes would be random, but that there might be some directionality for translocated rattlesnakes as they attempted to orient or even return. In fact, many of the successive movements of translocated rattlesnakes had a westerly component (the direction from which they had been moved). One explanation for this is that the snakes were able to orient in the direction of the monument using some form of navigation (see below), and another may be the use of topography in the translocation area. Many canyons that run westward toward Wet Beaver Creek bisect this region, and the area slopes down to the creek floodplain.

Changes in condition.—As expected, SVL and mass of *C. atrox* were strongly correlated in this study. Most snakes gained little length during the study, which is typical for mature snakes (Andrews, 1982), and rattlesnakes in particular (Fitch and Pisani, 1993). 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, peak just before hibernation, and decline during winter. This pattern of increasing mass during the summer foraging period and then losing mass over the winter months is typical for many reptile species in temperate climates, and is influenced by both endogenous and environmental factors (Andrews, 1982). Moore (1978) and Beck (1995) found that three rattlesnake species in southern Arizona increased foraging activity in the summer monsoon and in fall.

There was no obvious change in condition as a result of the translocation experiment in any of the *C. atrox* at MOCA. This may be due to the quality of the translocation site (translocated rattlesnakes were able to forage and hibernate successfully in this area). Four of six translocated snakes had greatly increased movement distances 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 increased energetic requirements associated with wandering behavior. This was the case in only one translocated snake. Loss in body condition after translocation has been seen in a variety of species, including *C. horridus* (Reinert and Rupert, 1999), Giant Tortoises (*Geochelone gigantea*; Hambler, 1994), Slow Worms (*Anguis fragilis*; Platenberg and Griffiths, 1999), Woodland Caribou

(*Rangifer tarandus*; Compton et al., 1995), Meadow Voles (*Microtus pennsylvanicus*; Otsfeld and Manson, 1996), and Kakapo (*Strigops habroptilus*; Lloyd and Powlesland, 1994). Decline in body condition is most often attributed to a decrease in food acquisition, a decrease in the overall amount of time spent foraging, and/or an increase in the amount of time spent in vigilance or exploring the new habitat (Wolf et al., 1996).

Blood samples need to be taken for the population at MOCA to determine whether snake-specific diseases or parasites exist in this population. Given his loss of condition and symptoms present at his death, it is possible that male 34 contracted paramyxovirus or some other disease after translocation, or that he was carrying a disease or parasite that became virulent only after the stress of being translocated to an unfamiliar area (Dodd and Seigel, 1991; Stephenson and Pisani, 1991; Davidson and Nettles, 1992; Cunningham, 1996). These hypotheses were not evaluated.

Mortality.—Adult rattlesnakes have few natural predators and consequently their mortality rates tend to be relatively low (averaging < 20%) in habitats not impacted by humans (Reinert and Rupert, 1999). Mortality rates of displaced rattlesnakes, however, are often three times greater than non-displaced individuals (Hare and McNally, 1997; Reinert and Rupert, 1999; B. Johnson, Metro Toronto Zoo, unpublished). This may result from increased frequency and distance of movements, movements at inappropriate times of the day and season, and/or inability to find suitable winter refugia. All of these factors expose snakes to increased pathogens and predation.

More than 50% of the translocated snakes at MOCA died or disappeared. With the exception of one snake (male 34), loss of condition did not appear to play a role in these mortalities. While there was no obvious link between these deaths and the act of translocation, these patterns are consistent with those seen in other studies. Increased mortality rates of displaced animals have been observed across vertebrate taxa (Hambler, 1994; Blanchard and Knight, 1995; Jones et al., 1997; Van Vuren et al., 1997; and Platenburg and Griffiths, 1999).

The areas selected for translocation were chosen because of limited human activity, and only one snake (female 43) was suspected to have died as a result of human activities. This area also contained suitable hibernation and foraging areas, and at least six of seven snakes survived their first post-translocation hibernation season, in contrast to a study on the Eastern Massasauga (*Sistrurus c. catenatus*; B. Johnson, unpublished). In spite of such screening, the ultimate survival rate of translocated snakes was not high. The deaths of two translocated snakes after successfully returning to MOCA (one found dead apparently well out of its normal range) make a strong case for long-term monitoring of translocated snakes (see Reinert and Rupert, 1999).

Homing abilities after translocation.—There appears to be a strong drive in displaced animals to return, often over huge distances, to areas that are familiar. For simplicity, we defined this behavior for rattlesnakes in this study as "homing." Over half of the rattlesnakes translocated in the MOCA study returned to their original activity ranges within two years of translocation. This high return rate was also seen in a rattlesnake translocation study at the Arizona-Sonora Desert Museum, Tucson, Arizona (Perry-Richardson and Ivanyi, 1992). Over 50% of the rattlesnakes released immediately adjacent to the museum returned, 15 to 20% released 1.5 km away returned, and at least one returned from being released 4 km away. Homing of translocated animals is common in other ectotherms. For example, non-migratory Brown Trout (*Salmo trutta*) returned over 150 m and up a different tributary to their capture site (Halvorsen and Stabell, 1990), Western Painted Turtles (*Chrysemys picta bellii*) returned over 8 km to their natal ponds (S. Orchard, pers. comm.), and Desert Striped Whipsnakes (*Masticophis t. taeniatus*) returned over 850 m to their hibernacula (Parker and Brown, 1980).

Homing may occur because familiar locations are predictable or ideal for successful foraging, hibernating, and/or mating. It is likely that for animals such as rattlesnakes, which have a relatively small activity range for which they exhibit site-fidelity, learning habitat parameters occurs at an early age. This hypothesis has apparently not been field-tested in snakes, but Heatwole (1977) and Reinert (1993) mentioned its potential importance. Alternatively, availability of water, hibernacula, and/or dense prey populations may be responsible for attracting displaced snakes back to MOCA. This would encourage the return of rattlesnakes that were translocated from the monument if the translocation area did not contain equally suitable areas for foraging or hibernating. We did not compare the relative abundance of prey at the translocation sites and on the monument, but it is possible that the riparian area and heavily used areas of human activity at MOCA may artificially increase prey populations (e.g., Graham, 1991).

It might be suggested that the translocated rattlesnakes at MOCA returned to the monument because they were already familiar with the translocation sites, but there is no evidence to support this hypothesis. It is unlikely that any of the subjects would have traveled to or from the translocation area prior to the experiment. In three seasons of study, no rattlesnake traveled more than 1 km during the course of its active season, nor was a greater straight-line movement seen for eight *C. atrox* telemetered at Tuzigoot National Monument (Verde Valley, Arizona) during the same time period (E. Nowak, unpublished). Further, none of the MOCA snakes returned to the monument immediately after translocation.

It is likely that the snakes spent time orienting within the translocation site before returning to their original activity range. The mechanisms that snakes use to orient and navigate, however, are not well understood (Fraker, 1970; Landreth, 1973; Newcomer et al., 1974; Parker and Brown, 1980; Gregory, 1984; Graves et al., 1986; Lawson, 1991; Halpern, 1992). There is increasing speculation, however, that the facial pits are capable of detecting long-distance radiant heat emissions (Berson and Hartline, 1988; Sexton et al., 1992). If this were substantiated, then the large limestone outcrop in which many residents hibernated would be an obvious navigational landmark. These cliffs are routinely several degrees Celsius warmer than the surrounding landscape during the day and emit discernible radiant heat during summer nights (E. Nowak, unpublished). Perhaps the snakes followed land contours and/or used olfactory cues (non-snake odors associated with certain biotic conditions), as at least two of the translocated rattlesnakes followed a large east-west running wash to the riparian area on the monument (see also Fraker, 1970; Klauber, 1972; Parker and Brown, 1980; Halpern, 1992). Another possibility is that our subjects followed the scent trails of other rattlesnakes to the monument (Graves et al., 1986; Ford, 1986; Reinert and Zappalorti, 1988b; but see King et al., 1983).

Not only did the translocated snakes return to the monument, they returned to the activity ranges they used before translocation, including some of the same refugia and hibernacula (Nowak, 1998). This observation adds further support to the conclusion that rattlesnakes exhibit strong site-fidelity to suitable hibernacula and foraging areas (Gregory, 1984; Sexton et al., 1992; Reinert, 1993). Homing to exact locations has been seen in other species of rattlesnakes (Perry-Richardson and Ivanyi, 1992; Hardy and Greene, 1999a) and in other snake species (Parker and Brown, 1980). Although it is possible that the returned rattlesnakes were found in the same areas by chance (e.g., Otsfeld and Manson, 1996), it is more likely that they were using the same cues to seek suitable sites they used before, perhaps relying on some internal "map" in combination with familiar structural or thermal landmarks (Newcomer et al., 1974; Sexton et al., 1992).

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 been documented in other studies of vertebrate translocation, where it has been tied to social factors and distance of displacement (Parker and Brown, 1980; Bright and Morris, 1994; Van Vuren et al., 1996; Hein and Whitaker, 1997; Jones et al., 1997). At MOCA, it is likely that these snakes did not return because they were able to meet all of their needs adequately in the translocation area. They were frequently located within the riparian area north of the monument, where they exhibited normal foraging behavior and found suitable hibernacula. Reinert and Rupert (1999) drew the same conclusions from successfully translocated *C. horridus* in Pennsylvania.

Extra-Experimental Effects.—For a thorough discussion of extra-experimental effects in this study, refer to Nowak (1998). However, some trends in these data warrant further discussion. Most male *C. atrox* at MOCA had larger activity ranges than females, although there was a high amount of variability among individuals. There was a trend in males to move a greater distance per day and a greater total distance than females, regardless of season. In general, male rattlesnakes tend to travel farther and are more active than females regardless of season (Gannon and Secoy, 1985; McCartney et al. 1988; King and Duvall, 1990; Brown, 1991; M. Goode, pers. comm.).

Year of study did not have a significant impact on condition of MOCA animals. This is somewhat surprising given that 1996 was a drought year (NOAA, 1996). As expected for rattlesnakes, there was a significant effect of sex on the relationship between SVL and mass (and on the residuals of this regression). In nearly all rattlesnake species, males tend to be longer, more muscular, and heavier than females (Shine, 1993; Beaupre, 1995). In the MOCA study, these sex differences may have obscured any differences in changes in condition between translocated and control snakes, or even within each group over time; however, there were insufficient numbers of females to permit separate analyses of condition by sex.

Translocation might affect the reproductive success of female rattlesnakes, especially if translocated during gestation to areas that do not contain rookeries suitable for gestation (see Graves et al., 1986; Hardy and Greene, 1999a). Subsequently, the young might have difficulty locating suitable hibernacula due to a lack of existing pheromone cues (e.g., Brown and Maclean, 1983; Ford, 1986; but see Reinert and Rupert, 1999).

TUCSON STUDY

MATERIALS AND METHODS

Study Site

The study area is largely upland Sonoran Desertscrub (Turner and Brown, 1994) characterized by Palo Verde (*Cercidium microphyllum*), Saguaro Cactus (*Carnegiea gigantean*), and Triangle-leaf Bursage (*Ambrosia deltoidea*). It is centered in RMFD District 77 near the City of Oro Valley (Pima County, Arizona), seven miles north of Tucson on the northwest flank of the Santa Catalina Mountains (Fig. 13). The study site is bordered by U. S. Forest Service land (Coronado National Forest) to the northwest and southeast, and bisected by State Route 77 and the Canada del Oro floodplain. The border property is composed of a mixture of natural vegetation and residential development. The study area was divided into four sites surrounding the fire station. All sites (particularly site 1) are used by hikers, horseback riders, off-road vehicles, as well as for firearm shooting, and other recreational activities. Illegal litter dumping and cactus removal also occur in these areas, and native vegetation is degraded in local patches. These three sites are located on a combination of private and city lands adjacent to residential areas. Site 4 was not included in this study and is discussed elsewhere (Hare and McNally, 1997).

Capture Methods

From November 1993 to August 1994, 97 rattlesnakes were processed after capture by firefighters. These included 93 *C. atrox* (58 males, 37 females, and two unsexed individuals), two adult male *C. m. molossus*, one adult male Mojave Rattlesnake (*C. s. scutulatus*), and one male Tiger Rattlesnake (*C. tigris*). Average male SVL in *C. atrox* was 83.6 cm (N = 57), and average female SVL was 79.2 cm (N = 36).

During processing, each snake was secured in a clear-plastic tube for safe handling and individually marked by injecting a passive integrated transponder (PIT) tag 11–12 cm anterior to the vent under the second or third dorsal scale row (Fagerstone and Johns, 1987; Jemison et al., 1995). The injection site was swabbed with Betadine or isopropyl alcohol prior to implantation, and it was closed with a cyanoacrylate sealer. The success rate of PIT-tag injections was 98%. Of 97 PIT-tagging attempts, implantation failure occurred only twice, rendering the transponders nonsterile and unusable. Individuals that appeared to be less than one year old were not PIT-tagged. All snakes captured by firefighters were scanned for the presence of PIT-tags until 1995. The scanner and data sheets were left at the fire station to encourage compliance with the study and firefighters were instructed to alert us of any recaptures.

Telemetry Methods

Telemetry materials are the same as those detailed in the MOCA section, with the following exceptions. Snakes were located with a Wildlife Materials (Carbondale, Ilinois) receiver. The PIT-tags, injectors, and Trovan LID 500 readers were obtained from InfoPet Identification Systems, Inc. (Norco, California).

Telemetry methods followed those of MOCA, with the following differences. Rattlesnakes were anesthetized using Halothane vapor at a veterinary hospital, and were observed from 24 to 72 h after surgery to ensure complete recovery. Data are presented as mean ± one standard deviation.

Translocation

From 1993 to 1994, marked snakes were translocated to one of four sites outside their original capture area (Fig. 13). In 1994 and 1995 nine adult rattlesnakes (three male and four female *C. atrox*, one male *C. tigris*, and one male *C. m. molossus*) were telemetered and translocated after recovery from surgery. (Results for the *C. tigris* and *C. m. molossus* will not be discussed in this paper; see Hare and McNally, 1997.) Two males and one female *C. atrox* were translocated to site 1, two females were translocated to site 2, and one male and one female were translocated to site 3. The fire station staff did not record the original location of each snake.

From 1994 to 1995, we tracked each snake twice weekly during the active season, and once weekly during winter. We attempted to locate each snake from three to 36 times ($\bar{x}$ = 20 ± 11). The number of times each snake's location was determined varied between two and 22 ($\bar{x}$ = 11 ± 6). In order to minimize distur-

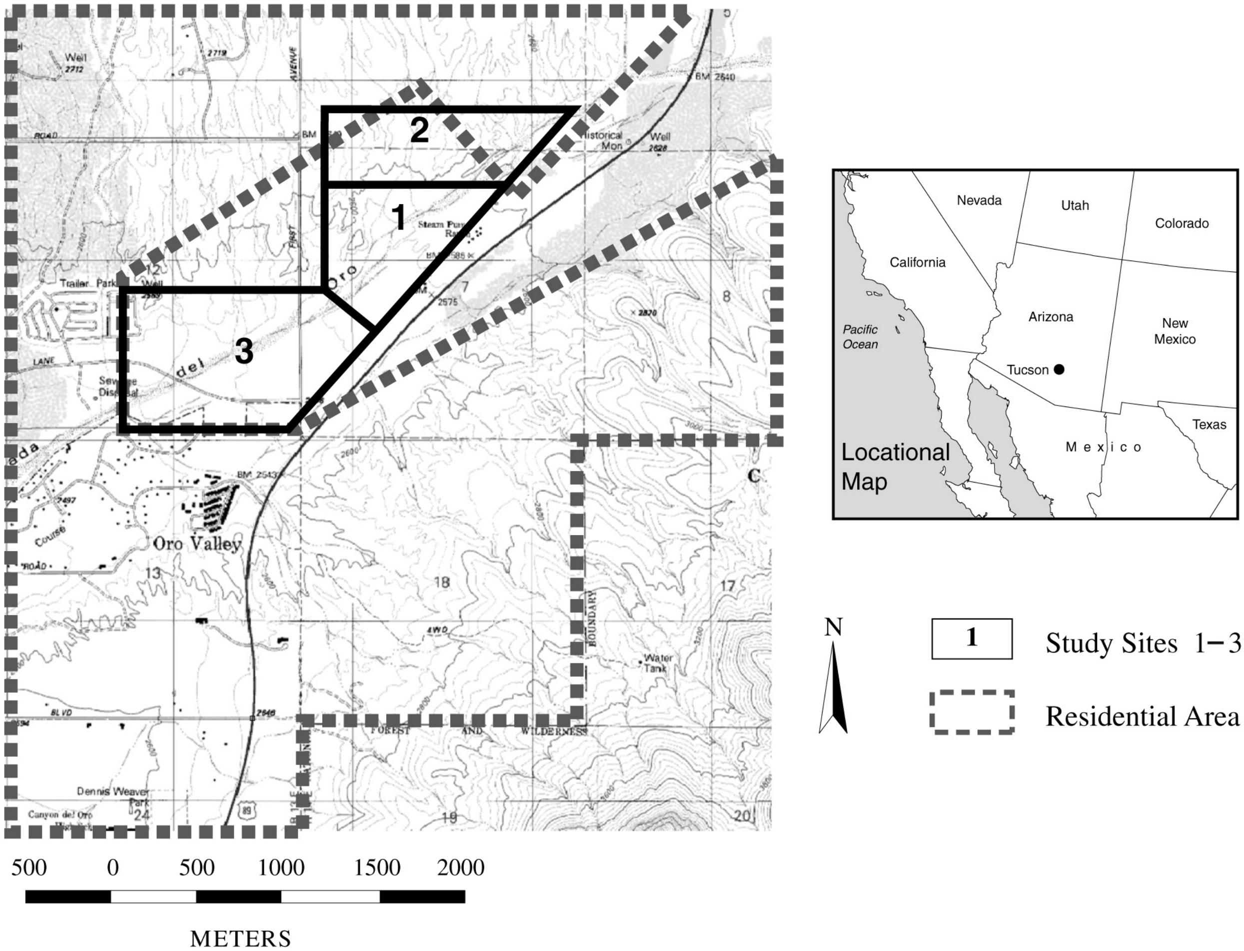

Figure 13. Tucson study sites for translocation research for *Crotalus* spp. from 1993 to 1995.

bance snakes were not routinely recaptured and were observed from a distance. Date, location, and whether the snake was visible were noted each time that a snake location was pinpointed. Locations were marked, identified in field notes, and plotted on 1" to 20' aerial photographs. Distances traveled between pinpointed locations were determined from the plots in the movement analysis software and concurred with distances derived in the field.

Paramyxovirus Titering

Recognizing the potential of translocation as a vector for disease transmission, particularly ophidian paramyxovirus (Jacobson and Gaskin, 1992), we conducted a survey of humoral antibody response to viperid paramyxovirus. An experienced veterinarian collected ≥ 2 ml of blood from each of 20 randomly selected non-telemetered snakes. As both replication of viperid paramyxovirus and reptile immune response are temperature-dependent, and latent infections may be activated at a later date, samples were taken throughout the year (Marcus, 1971; Lunger and Clark, 1979; Peterson et al., 1993). Each sample was tested for viperid paramyxovirus serologic titer at the Veterinary College of the University of Florida, Gainesville (after Jacobson and Gaskin, 1992). These snakes were held for 24 h before release with no adverse reactions noted.

Data Analyses and Presentation

Data analyses follow those of MOCA, but with several exceptions. For example, there were no comparisons of translocated to control parameters. To estimate the activity range size for each snake, we used the minimum convex polygon method (White and Garrott, 1990) in the computer program McPAAL (Micro Computer Program for Analyzing Animal Locations; M. Stüwe, National Zoological Park, Virginia). In contrast to the MOCA data, home range data were not standardized by a minimal number of locations. The movement data were not standardized by defining a minimal movement distance or by

Table 1. Summary of activity range (ha) and average distance traveled per day (m/day) by translocated rattlesnakes in the Tucson Rural Metro Fire Department, AZ, between April 1994 and July 1995. Snake number, species, sex, percent time a signal was located out of the total number of attempts, total distance moved (m), and duration of tracking (days) are listed for each individual. * = across all seasons.

Snake number	565	605.1	625	646	665	685
Sex	M	F	F	M	M	F
Activity range (ha)	8.80	10.98	1.65	16.99	27.74	12.00
% signal locations	31	86	67	58	59	64
Total distance moved (m)	1337	1511	618	1764	1520	1905
Days followed	378	91	87	181	370	395
Average distance/day*	3.6	16.6	7.1	9.7	4.1	4.8
Average distance/day						
Spring ’94	—	22.7	—	—	—	17.5
Dry Summer	3.5	14.3	7.1	8.2	19.0	4.9
Wet Summer	0.4	Predated	Crushed	11.3	0.7	2.2
Fall	11.9	—	—	Predated	5.0	9.5
Winter	2.7	—	—	—	0.0	1.6
Spring ’95	2.8	—	—	—	4.7	5.2
Dry Summer	4.7	—	—	—	6.3	Lost

excluding movements more than four days apart. Average distance moved per day was calculated by dividing the distance between successive locations by the number of days between successive locations without setting conditions for a minimum movement. Further, we analyzed the movements of translocated snakes by season as defined for MOCA, with the addition of a winter period from December to February. Changes in condition were not analyzed.

RESULTS

Additional information on the movements of individual telemetered snakes and their behavior and ecology is found elsewhere (Hare and McNally, 1997). One telemetered male *C. atrox* was located twice before he was lost, and thus is not included in the analyses.

Activity range size.—The activity range size of the translocated rattlesnakes varied greatly, in part dependent on the number of times each animal was located after translocation (Table 1). The average activity range of the *C. atrox* at this site was 13.02 ± 8.77 ha (N = 6). Activity range sizes for males averaged 17.84 ± 9.50 ha (N = 3), and for females averaged 8.21 ± 5.07 ha (N = 3).

Average distance moved per day.—The average distance moved per day for each rattlesnake tracked is shown in Table 1. Those data were collected over longer intervals than at MOCA (every three to four days compared to every two to three days for MOCA) so the two cannot be compared. Nonetheless, MOCA data from 1996 are similar to this study. As expected given the larger activity ranges of the MOCA snakes, the 1996 average movements per day are obviously longer than for the Tucson snakes. For the six translocated *C. atrox* in Tucson, the average distance moved per day after translocation was 7.65 ± 4.93 m/day.

Male *C. atrox* moved an average of 5.8 ± 3.39 m/day, and females moved 9.5 ± 6.25 m/day. Overall, *C. atrox* moved an average of 9.5 ± 6.0 m/day in the dry summer of 1995 (N = 6), 3.65 ± 5.16 m/day in the wet summer (N = 4), 8.8 ± 3.50 m/d in the fall, 1.43 ± 1.35 m/day in the winter (N = 3), and 4.23 ±1.27 m/day in spring 1996 (N = 3).

Total distance traveled.—The estimated total distance moved by translocated male *C. atrox* in the Tucson study (excluding the snake lost after two weeks) ranged from 1.5 to 1.7 km, while distances for translocated female *C. atrox* in this study ranged from 0.6 to 1.9 km (Table 1). A careful examination of Table 1 shows that the actual distances traveled by the Tucson snakes may be much farther. Transmitter signals were heard on 57% of the days location was attempted, suggesting that the snakes were out of range on 43% of attempted locations.

Changes in body condition.—Only one snake (a non-telemetered female *C. atrox*) was measured (SVL, mass) after being recaptured post-translocation. This snake did not have any perceptible increase in SVL and her mass on recapture reflected a loss of 23.9 g (6.5%) over ca. six months. She was not known to be pregnant at either capture time.

Ophidian paramyxovirus.—All 20 blood samples assayed for viperid paramyxovirus had serology titers of ≤ 1:10. Serology titers of > 1:20 are considered positive; therefore, these assays indicated that the animals studied had no prior exposure to viperid paramyxovirus.

Mortality.—Five of seven telemetered *C. atrox* (71%) died or were lost. Two (one male and one female) were lost, and three suffered attack or predation. Of the latter, female 625 was likely buried by 2 m of dirt during a clearing and grading operation. Male 646 was found dead (human-caused) 2.2 km north of his last known location. Female 605.1 was likely killed by a Badger (Hare and McNally, 1997). In addition to the above deaths, one marked *C. atrox* was killed by a hunter who found the PIT-tag while skinning the snake and turned it into the Arizona Game and Fish Department in July 1995.

Recaptures after translocation.—Documentation of homing was not possible, as the original capture point of each snake was not recorded. Three of 97 (3%) marked *C. atrox* were recaptured during the study period. One female made a straight-line movement of ca. 1 km from her release in site 3 in April 1994, to her capture site in October 1994. A male originally released at site 2 in July 1994, was recaptured ca. one month later, but unfortunately its place of recapture was not recorded. The Arizona Game and Fish Department reported the third snake after a hunter who killed it (site 1) brought in its PIT-tag.

DISCUSSION

Changes in activity range size.—Size of activity ranges for the Tucson *C. atrox* are ca. 30% larger than those previously recorded for free-ranging *C. atrox* in southern Arizona (Beck, 1995). Published reports of average activity range size in other rattlesnake species tracked for at least a year include: 21 ha for Sidewinders (*Crotalus cerastes*; Secor, 1994), 25 ha for *S. c. catenatus* (Weatherhead and Prior, 1992), 27 ha for *C. horridus* in New Jersey (Reinert and Zappalorti, 1988a), and 59.9 ha for *C. horridus* in Pennsylvania (Reinert and Rupert, 1999). The average activity range of the translocated Tucson *C. atrox* was also smaller than that of translocated MOCA *C. atrox*.

Changes in movement patterns.—The distances made by translocated Tucson *C. atrox* were not as great as either of the MOCA treatment groups. Also, we found that activity ranges and the distance moved per day were smaller than those reported for MOCA snakes. Thus, we feel the differences between our reported movement parameters are primarily attributable to differences in habitat, elevation, and human-mediated disturbance factors.

As in the MOCA translocated snakes, several of the Tucson rattlesnakes exhibited wandering behavior, as evidenced by the comparatively long distances covered by the snakes after translocation. We also interpret the difficulty associated with regularly locating telemetered individuals to mean that individuals were regularly moving out of range of the receiver. These results are similar to those seen during a study of translocation of telemetered *C. viridis* at Scotts Bluff National Monument, Nebraska (D. Virchow, pers. comm.). During that study, two snakes were lost the day after release (no signals were subsequently detected), and one snake traveled 250 m from the release site before disappearing.

One non-pregnant female *C. atrox* made very few movements after translocation. This behavior is similar to that seen for a translocated MOCA female. Hypotheses potentially explaining this seemingly aberrant movement pattern are discussed in the MOCA section.

Ophidian paramyxovirus and disease.—Translocated vertebrates have been demonstrated to negatively impact resident wildlife populations via disease transmission (reviewed by Dodd and Seigel, 1991; Davidson and Nettles, 1992; Cunningham, 1996). Viperid paramyxovirus is spread readily from snake-to-snake through contact with body fluids or exhaled viral particles of infected animals (Jacobson and Gaskin, 1992; Odum and Goode, 1994). Thus, the disease is a concern during translocation of rattlesnakes, especially where individuals are routinely carried in the same holding containers. This practice is common where rattlesnakes are repeatedly translocated in public settings, such as residential areas.

None of the Tucson rattlesnakes tested positive for exposure to ophidian paramyxovirus. We suspect that this virus either is not present or is uncommon in rattlesnakes in our study population. However, given that over 4,000 snakes per year are translocated, and we tested only 20, it is possible that paramyxovirus may be an as-yet undetected or latent problem in the Tucson area.

Mortality.—Over 70% of the telemetered Tucson *C. atrox* either died or were lost. This may indicate increased susceptibility to predation both by humans and other animals after translocation in an urban setting, though depredation rates on non-translocated snakes were not available for comparison. Humans depredated at least three snakes. All of these snakes used habitats that were heavily degraded by humans and contained exotic species of plants and animals and scattered debris piles. Most snake populations rely on high adult survivorship and adult snakes usually suffer much lower mortality rates than those documented for the Tucson study animals. For comparison, Fitch and Pisani (1993) estimated an annual adult mortality rate of 20% in their study population of *C. atrox*. Other authors have implicated areas of heavy human activity as a main source of adult snake mortality (Greene, 1992; Gibbons et al., 2000). Rattlesnake survivorship may be notably compromised by human encroachment in snake habitat (Galligan and Dunson, 1979; Seigel, 1986; Harding, 1991; Dodd, 1993; Rosen and Lowe, 1994; Greene, 1999).

Recaptures.—Only 3% of marked snakes were recaptured alive during the study period. This can be interpreted to mean that 97% of the snakes were managed without compromising public safety. However, four telemetered snakes were tracked to residential areas seven times without independent detection by local property owners (Hare and McNally, 1997). One snake was located ca. 1 m from the front door of a residence without independent detection by the occupants.

These results are consistent with those from the MOCA study (Nowak, 1998). Discounting the original capture of snakes in human use areas at MOCA, the total number of subsequent independent sightings of telemetered *C. atrox* was less than 10 of over several hundred sightings. In several cases rattlesnakes were located less than 5 m from visitor trails within view of hundreds of visitors that day, and yet were not detected until revealed by researchers. Our observations suggest that the potential for encounters with nuisance and/or subsequently translocated animals exceeds the recorded occurrence.

Extra-experimental effects.—Extra-experimental effects for the Tucson study are discussed in detail in Hare and McNally (1997). Briefly, Tucson male *C. atrox* moved both less per day and per season than females, in contrast to MOCA males, but this result is likely an artifact of small sample size. Other researchers have shown that rattlesnakes, particularly males, move longer distances per day in the spring and fall, due either to migratory dispersal or to increase mating opportunities (Landreth, 1973; Duvall et al., 1985; Seigel, 1986; Beck, 1995). This was not a significant pattern in the Tucson study, although there was a trend for farther movements during those time periods.

GENERAL DISCUSSION

Translocation Effects

Aberrant or modified activity patterns in displaced Western Diamond-backed Rattlesnakes (*C. atrox*) and other snake species have been thoroughly documented over the past 30 years (Fitch and Shirer, 1971; Landreth, 1973; Galligan and Dunson, 1979; Graham, 1991; Sealy, 1997, this volume; Reinert and Rupert, 1999). We observed the same trends in translocated rattlesnakes at our two study sites in Arizona. Although there were few statistically significant impacts on movement patterns, behavior, or condition, more than 50% of the translocated snakes exhibited increased ranges and wandering behavior.

At both of our study sites, over half of the translocated snakes died or were lost. The mortality rate was higher for the Tucson snakes, likely due to a greater degree of human encroachment. The high mortality rates observed in both our studies suggests that long-distance translocation (LDT), as it is currently practiced, may not be humanitarian despite conventional wisdom among management agencies and private citizens to the contrary.

The population-level effects of translocation on rattlesnakes have not yet been addressed in any study, but obviously are important when considering the general issue of animal translocation. What are the impacts of translocations on resident rattlesnakes in the translocation area, particularly when large numbers of rattlesnakes are continuously displaced to the same area? If rattlesnakes are translocated outside their normal activity range, they could be introduced into a habitat where population density is high, and could be forced to move to a new area (Hare and McNally, 1997). On the other hand, they could also be introduced into habitats that do not contain rattlesnakes because existing conditions are unsuitable for their persistence (D. Hardy, Sr., pers. comm.). Either outcome could increase the probability of natural predation and human-induced mortality, result in disease transmission, and/or decrease foraging and interfere with various aspects of the mating system, such as reproductive success (Dodd and Seigel, 1991; Davidson and Nettles, 1992; Duvall et. al, 1992; Cunningham, 1996; Wolf et al., 1996; Whiting, 1997). In addition, Reinert (1991) observed a translocated male *C. horridus* being courted by a previously normally-behaving resident male, suggesting the social behaviors of resident populations may be negatively affected by translocated snakes. Male-male “courtship” after translocation has been documented in other snake species (Fitch and Shirer, 1971; Galligan and Dunson, 1979).

In addition to effects on conspecifics, the ecological impacts of rattlesnake translocation on rattlesnake predators and prey might be significant when repeated translocations of rattlesnakes occur in small areas, exacerbating the factors discussed above. Rattlesnakes translocated more than a few meters by public land managers and removal agencies are typically released into a few "favorite" locations (G. Good, pers. comm.; S. Sandell, pers. comm.).

An extremely important result of our research is that more than 50% of the translocated MOCA *C. atrox* returned to the monument. The ability of rattlesnakes to return over long distances to their original activity ranges after being displaced suggests that LDT is not an effective long-term management tool for decreasing rattlesnake-human interactions in public or residential areas. While translocation of rattlesnakes more than five miles would likely be effective at decreasing interactions of those individuals with people, this hardly seems a sustainable long-term solution to the problem.

Creation of Nuisance Rattlesnakes

Although our studies focused on determining the effects of translocation on rattlesnakes, we also gained valuable insight into the overall issue of rattlesnake-human interactions. There are both proximate and ultimate reasons for rattlesnakes becoming nuisances, and there is a strong human component to this label.

Rattlesnake presence in human use areas.—Rattlesnakes may be present in some public and residential areas during spring and fall due to the proximity of these areas to potential hibernacula (= dens) (Nowak, 1998). During migrations to and from dens, at least three MOCA rattlesnakes usually traveled through the visitor and/or housing areas. In addition, over 50% of the MOCA rattlesnakes were hibernating in dens less than 100 m from the main visitor trail, a n occurrence documented in other national parks. A study at Natural Bridges National Monument, Utah, 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 (Graham, 1991).

Another reason for rattlesnake presence in human use areas may be foraging opportunities for snakes in summer. In a study of *C. viridis*, Graham (1991) observed that there was an increased abundance of potential prey (rodents, lizards, and birds) around the visitor center and housing areas at Natural Bridges National Monument, compared to other areas nearby. He suggested that the increased abundance of prey in visitor and housing areas might be due to the presence of non-native vegetation, 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 by snake prey. Artificially increased prey abundance and the presence of artificial refugia (e.g., under buildings) are cited as potentially important influences of rattlesnake distribution at the Arizona-Sonora Desert Museum (Perry-Richardson and Ivanyi, 1992). In rural and suburban areas of southern Arizona, wildlife feeding and watering stations (including backyard bird feeders) have been documented to attract rattlesnakes to drink and feed on bird and small mammals (M. Goode, pers. comm.; D. Hardy, Sr., pers. comm.).

Twelve of 19 (63%) of telemetered MOCA rattlesnakes were located in either visitor access or housing areas at least once during their active period (Nowak, 1998). It is not known, however, whether prey concentration around human use areas at MOCA 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.

Procrypsis.—In spite of a relatively high frequency of locations of rattlesnakes by researchers in human use areas in our studies, the snakes were almost never seen by other humans. In general rattlesnakes are rarely detected because they are usually hesitant to rattle when confronted by predators (including humans), and instead rely on procrypsis to escape detection. Procryptic behavior has been independently documented for a number of rattlesnake species across North America (Klauber, 1972; Duvall et al., 1985, unpublished; Graham, 1991; Prior and Weatherhead 1994; May et al., 1996; Parent and Weatherhead, 2000). Procrypsis may be an especially adaptive trait in areas with long histories of continual human use, such as MOCA and Tucson (C. Fincher, pers. comm.).

Individual rattlesnakes foraging in or traveling through concentrated human use areas may be habituated to the presence of people and less likely to display defensive behaviors. Some MOCA rattlesnakes, however, seemed to follow circuitous paths to avoid these areas (Nowak, 1998). These avoidance behaviors may be triggered by the presence of over 900,000 people annually and/or by an earlier capture by park staff, or by some learned cultural tradition as a result of the long-term human occupation of this area (Klauber, 1972; Sealy, 1997; Parent and Weatherhead, 2000). Sealy (1997; this volume) suggested that *C. horridus* translocated short distances are likely to avoid these capture sites in the future. Physical or temporal avoidance of areas regularly visited by humans has been noted for *C. horridus* (Brown, 1993). Although Parent and Weatherhead (2000) found that *S. c. catenatus* at a heavily-visited national park in Canada did not abandon preferred habitat in visitor use areas, movements of snakes in these areas were shorter and less frequent when compared to those in undisturbed sites.

Human perceptions of rattlesnakes.—A lack of basic understanding and an innate fear of snakes has led to widespread mistrust and persecution of these animals (Greene and Campbell, 1992; Wilson, 1996; Greene, 1997, 1999). Exaggerated beliefs about the danger posed by rattlesnakes, combined with misunderstanding factors that influencing rattlesnake distribution, have led to the expectation that rattlesnakes will be removed from or killed in areas where they are likely to come into contact with humans.

Rattlesnakes at our study sites did not strike at volunteers, park staff, or researchers unless handled or cornered (see Hardy, 1986; Dart et al., 1992). In recorded incidents when Tucson snakes came into close proximity with human structures without being detected by the residents, or when MOCA snakes were located close to trails but not detected by visitors, no dangerous or adverse incidents occurred. Fifty to 75% of all venomous snakebites in the United States are "illegitimate" in that they occur after the victim recognizes that the snake is venomous and continues the interaction (Hardy, 1986; Curry et al., 1988; Dart et al., 1992; J. McNally, unpublished). A majority of southwestern national parks have had few to no snakebites in the last 25 years, and most bites have been illegitimate. There have been only two (nonlethal) envenomations in MOCA's history: (1) a child who stepped on an immature rattlesnake, and (2) a researcher who was PIT-tagging an immature rattlesnake. This suggests that unless inadvertently stepped on or handled, rattlesnake presence near areas of human use poses a minimal threat to their safety. Further, discouraging handling of rattlesnakes should be emphasized as a primary factor in preventing snakebite.

When people are educated about rattlesnake behavior and biology and human roles in encouraging nuisance behavior their attitudes often change (Duvall et al., unpublished; Greene, 1997, 1999). As the public becomes more tolerant of rattlesnakes, concerns regarding their removal are decreased and interest in their protection is increased. The importance of using education to lower the need for rattlesnake translocations cannot be overstated. As wildlife habitat outside public land refuges shrinks, rattlesnake populations are becoming increasingly threatened by new residential development replacing their habitats. Learning to accept the inevitable presence of rattlesnakes in transitional habitat adjacent to human-modified environments may contribute the most to the welfare of humans and snakes.

CONCLUSIONS AND FUTURE DIRECTIONS

When dealing with nuisance rattlesnakes in public use situations or 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 high concentration of rattlesnake prey due to human activities, landscape modification, or is near suitable hibernacula, then such an area is likely attractive to rattlesnakes. Continuous translocation of individual snakes from these areas may not decrease the number of rattlesnakes in the area (except in the immediate future). More snakes may immigrate to take advantage of the concentrated prey base or hibernacula, and translocated snakes are likely to return if possible. One long-term solution to rattlesnake-human conflicts would be to make such microhabitats less attractive to rattlesnake prey during the foraging season. If the area is near suitable hibernacula, rattlesnakes could be physically re-routed around human use areas or human traffic could be redirected from the migratory paths of the snakes (e.g., by creating elevated walkways for visitors).

Because our research has demonstrated that LDT has negative effects on rattlesnakes, and that translocated individuals are capable of homing over long distances, LDT should not be used to manage rattlesnake-human interactions. Short-distance translocation (SDT) of rattlesnakes into suitable habitat, preferably less than 50 m from their capture point, will decrease the immediate threat of negative interactions between rattlesnakes and people. Survival of rattlesnakes in urbanized environments may be decreased by SDT (Sealy, 1997; this volume) and enhance the persistence of natural ecosystem processes. It is also more cost- and time-effective than LDT. Although SDT is a highly recommended conservation measure, it is not always possible due to complicated social and economic pressures. Practically speaking, a nuisance snake would need to be translocated to the edge of the same parcel of property where it was captured as tremendous liability would exist in removing the snake from one home and placing it at another. The Arizona-Sonora Desert Museum replaced LDT in favor of SDT and has had a much higher recapture rate (as high as 87%) with no reported adverse interactions between humans and rattlesnakes (C. Ivanyi, pers. comm.). In the town of Portal (Cochise County, Arizona), SDT was instituted after years of LDT, studied, and then suspended as recaptures increased potentially increasing risks to the residents (Hardy and Greene, 1999a). We encourage more research and policy implementation that can balance the needs of wild venomous animals and humans in environments that are urbanized or under development.

To discourage wandering behavior, rattlesnakes should not be translocated farther than 1 km. Translocation should occur away from heavily-used roads and to similar habitats from which they were captured, which requires the translocating agency to have general knowledge of the habitat requirements of each species. This is particularly important for species with specialized habitat requirements, such as *C. cerastes* (Secor, 1994). In this scenario, snakes are simply removed to adequate vegetative cover where they are likely to continue their movements without again encountering humans. Translocation is most effective when the direction of the snake path is likely duplicated. During migration periods snakes should be moved toward potential hibernacula in fall and away from hibernacula in spring.

We recommend that agencies involved in translocations take a more active role to understand the biology of nuisance species (e.g., information on translocated individuals). Viperid paramyxovirus has been documented in wild populations of U. S. rattlesnakes (J. Jarchow, pers. comm.), and minimizing its threat should be a priority in all translocation programs. Selected coordinators should standardize the data collected on each translocated snake, recording at a minimum the location of capture, species, and release site. We suggest that a minimum of 10 ha should be provided for each translocated rattlesnake; this distance between translocations was subjectively derived by us (Hare and McNally). Implementing this suggestion will require more systematic planning and record keeping by the agency handling translocations, but may avoid overburdening a specific release site.

Finally, one of the most effective long-term solutions to rattlesnake-human conflicts will be education. Any agency responsible for nuisance wildlife removal will serve their subscribers best by participating in public education efforts focused on enhancing understanding and appreciation of these animals, decreasing activities that promote nuisance snake behavior, and proper handling of a snake encounter. Learning to accept the inevitable presence of rattlesnakes in human-modified environments may contribute the most to the welfare of humans and snakes, and ultimately reduce the desire for their translocation.

Acknowledgments.—Many people and organizations contributed to the success of these projects. Nowak's study was funded by the Southwest Parks and Monuments Association, the Southern Arizona Group office of the National Park Service, and Montezuma Castle National Monument. Her research was conducted under Northern Arizona IACUC regulations, Arizona Game and Fish scientific collecting permits, and by permission of the US Forest Service (Beaver Creek Ranger District). Almost every staff member of MOCA contributed to this project, and we would like to particularly thank Glen Henderson, Superintendent, and Kathy Davis, Resource Management Specialist, for their ongoing support of rattlesnake research at MOCA. Field and/or technical assistance was provided by Terry Arundel, Lee Benson, Christy Bumgarner, Valerie Coombs, Ann DaVega, Paul Deshler, John Goodwin, John Grahame, Jeff Larson, Gary Lollman, Jay Meyers, Manuel Santana-Bendix, Matthew Spille, and Maureen Stuart. Bruce Weber and the staff of the Verde Veterinary Hospital performed the snake implantation surgeries, while Canyonlands National Park provided several radio transmitters. Many other individuals provided helpful comments and/or field observations, including: Thurburn Barker, Mary Blasing, Steve Beaupre, Charles Drost, David Duvall, Matt Goode, John Grahame, Harry Greene, David Hardy, Sr., Andy Holycross, Tim Graham, Bob Johnson, Robert Manasek, W. "Marty" Martin, David Mauger, Kiisa Nishikawa, Jack O'Leile, Stan Orchard, Chris Parent, Janice Perry, Ben Porchuk, F. Harvey Pough, Bob Reed, Howard Reinert, Roger Repp, Phil Rosen, Matthew Rowe, Barbara Savitzky, Gordon Schuett, Cecil Schwalbe, John Sealy, Don Swann, Walt Timmerman, Charles van Riper III, Dallas Virchow, and Mark Wotawa. Hare and McNally's study was supported by the authors, the Arizona Poison and Drug Information Center, the Tucson Herpetological Society, and the Arizona Game and Fish Department. Our thanks go to Jim Jarchow, David Hardy, Sr., Matt Goode, Cecil Schwalbe, George Good, and Rodger Dougherty (RMFD). Tyler Hansen, Holly McNally, Kyle McNally, Cassidy Hare, and Delaney Hare were our field crew. Hare and McNally especially thank our wives, Janet Hare and Shawne McNally, who allow us to play with dangerous animals. An anonymous reviewer, Corey Fincher, David Hardy, Sr., Trevor Persons, and Gordon Schuett provided valuable suggestions for improving the manuscript.

Literature Cited

Andrews, R. M. 1982. Patterns of growth in reptiles. Pp. 273–320 *In* C. Gans and F. H. Pough (Eds.), Biology of the Reptilia, Vol. 13. Academic Press, New York and London.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, London.

Beaupre, S. J. 1995. Sexual size dimorphism in the western diamondback rattlesnake (*Crotalus atrox*): integrating natural history, behavior, and physiology. Sonoran Herpetol. 8:112–121.

Beck, D. D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. J. Herpetol. 29:211–223.

Berson, D. M., and P. H. Hartline. 1988. A tecto-rotundo-telencephalic pathway in the rattlesnake: evidence for a forebrain representation of the infrared sense. J. Neurosci. 8:1074–1088.

Blanchard, B., and R. Knight. 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. J. Wildl. Mgmt. 59:560–565.

Brammer, T. J., P. T. Bromley, and R. Wilson. 1994. The status of nuisance wildlife policy in the United States. Proc. Annu. Conf. Southeast Assn. Fish and Wild. Agencies 48:331–335.

Briggs, M. K., J. Howe, L. Harris, and W. Halvorsen. 1996. Using long-term monitoring to understand how adjacent land development affects natural areas: an example from Saguaro National Park, Arizona (US). Nat. Areas J. 16:354–361.

Bright, P. W., and P. A. Morris. 1994. Animal translocation for conservation: performance of doormice in relation to release methods, origin, and season. J. Appl. Ecol. 31:699–708.

Brown, W. S. 1991. Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. Herpetologica 47:101–115.

———. 1993. Biology, Status, and Management of the Timber Rattlesnake (*Crotalus horridus*): A Guide for Cnservation. Society for the Study of Amphibians and Reptiles, Herpetol. Circ. 22.

———, and F. M. MacLean. 1983. Conspecific scent trailing by newborn timber rattlesnakes, *Crotalus horridus*. Herpetologica 39:430–436.

Compton, B. B., P. Zager, and G. Servheen. 1995. Survival and mortality of translocated woodland caribou. Wildl. Soc. Bull. 23:490–496.

Cunningham, A. A. 1996. Disease risks of wildlife translocations. Conserv. Biol. 10:349–353.

Curry, S. C., D. Horning, P. Brady, R. Requa, D. B. Kunkel, and M. V. Vance. 1989. The legitimacy of rattlesnake bites in central Arizona. Ann. Emerg. Med. 18:658–663.

Dart, R. C., J. T. McNally, D. W. Spaite, and R. Gustafson. 1992. The sequelae of pitviper poisoning in the United States. Pp. 395–404 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

Davidson, W. R., and V. F. Nettles. 1992. Translocation of wildlife: identifying and evaluating disease risks. Transactions of the 57th North American Wildlife and Natural Resources Conference 1992:466–473.

Dodd, C. K., Jr. 1993. Strategies for snake conservation, Pp. 363–393 *In* R. A. Seigel and J. T. Collins (Eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York.

———, and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47: 336–350.

Duvall, D., S. J. Arnold, and G. W. Schuett. 1992. Pitviper mating systems: ecological potential, sexual selection, and microevolution. Pp. 321–336 *In* J. A. Campbell and E. D. Brodie, Jr., (Eds.) Biology of the Pitvipers. Selva, Tyler, Texas.

———, M. J. Goode, W. K. Hayes, J. K. Leonhardt, and D. G. Brown. 1990. Prairie rattlesnake vernal migration: field experimental analyses and survival value. Nat. Geogr. Res. 6:457–469.

———, M. B. King, and K. J. Gutzwiller. 1985. Behavioral ecology and ethology of the prairie rattlesnake. Nat. Geogr. Res. 1:80–111.

———, AND G. W. SCHUETT. 1997. Straight-line movement and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. Anim. Behav. 54:329–334.

FAGERSTONE, K. A., AND B. E. JOHNS. 1987. Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife. J. Wildl. Mgmt. 51:294–297.

FITCH, H. S., AND G. R. PISANI. 1993. Life history traits of the western diamondback rattlesnake (*Crotalus atrox*) studied from roundup samples in Oklahoma. Occ. Pap. Mus. Nat. Hist. Univ. Kansas, Lawrence 156:1–24.

———, H. S., AND W. SHIRER. 1971. A radiotelemetric study of spatial relationships in some common snakes. Copeia 1971:118–128.

FORD, N. B. 1986. The role of pheromone trails in the sociobiology of snakes. P.. 261–283 *In* D. Duvall, D. Muller-Schwarze, and R. M Silverstein (Eds.), Chemical Signals in Vertebrates 4. Plenum Press, New York.

FRAKER, M. A. 1970. Home range and homing in the watersnake, *Natrix sipedon sipedon.* Copeia 1970:665–673.

GALLIGAN, J., AND W. DUNSON. 1979. Biology and status of timber rattlesnake (*Crotalus horridus*) populations in Pennsylvania. Biol. Conserv. 15:13–58.

GANNON, V. P., AND D. M. SECOY. 1985. Seasonal and daily activity patterns in a Canadian population of the prairie rattlesnake, *Crotalus v. viridis*. Can. J. Zool. 63:86–91.

GIBBONS, J. W., D. E. SCOTT, T. J. RYAN, K. A BUHLMANN, T. D. TUBERVILLE, B. S. METTS, J. L. GREENE, T. MILLS, Y. LEIDEN, S. POPPY, AND C. T. WINNE. 2000. The global decline of reptiles, deja vu amphibians. BioScience 50:653–666.

GRAHAM, T. 1991. Western rattlesnake ecology at Natural Bridges N. M., Utah. Park Science 11:10–11

GRAVES, B. M., D. DUVALL, M. B. KING, S. L. LINDSTEDT, AND W. A. GERN. 1986. Initial den location by neonatal prairie rattlesnakes: functions, causes, and natural history in chemical ecology. Pp. 285–304 *In* D. Duvall, D. Muller-Schwarze, and R. Silverstein (Eds.), Chemical Signals in Vertebrates 4. Plenum Press, New York.

GREENE, H. W. 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley and Los Angeles.

———. 1999. Living with snakes. Pp. xv–xix *In* G. H. Rodda, Y. Sawai, D. Chizar, and T. Tanaka (Eds.), Problem Snake Management: The Habu and the Brown Treesnake. Cornell University Press, Ithaca, New York.

———, AND J. A. CAMPBELL. 1992. The future of pitvipers. Pp. 421–428 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

GREGORY, P. T. 1984. Communal denning in snakes. Pp. 57–75 *In* R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malaret, and N.L. Zuschlag (Eds.), Vertebrate Ecology and Systematics - A tribute to Henry S. Fitch. Museum of Natural History, University of Kansas, Lawrence.

HALPERN, M. 1992. Nasal chemical senses in reptiles: structure and function. Pp. 423–523 *In* C. Gans, and D. Crews (Eds.), Biology of the Reptilia, Vol.18. The University of Chicago Press, Chicago.

HALVORSEN, M., AND O. B. STABELL. 1990. Homing behaviour of displaced stream-dwelling brown trout. Anim. Behav. 39:1089–1097.

HAMBLER, C. 1994. Giant tortoise (*Geochelone gigantea*) translocation to Curieuse Island (Seychelles): success or failure? Biol. Conserv. 69:293–299.

HARDING, J. H. 1991. Comments on herpetological collecting: the need for considering life history data in management and regulatory planning. Bull. Chicago Herpetol. Soc. 26:157–159.

HARDY, D. L., SR. 1986. Fatal rattlesnake envenomation in Arizona: 1969–1984. Clin. Toxicol. 24:1–10.

———, AND H. W. GREENE. 1999a. Borderland blacktails: radiotelemetry, natural history, and living with venomous snakes. Pp. 117–121 *In* G. J. Gottfried, L. G. Eskew, C. G. Curtin, and C. B. Edminster (Eds.), Toward Integrated Research, Land Management, and Ecosystem Protection in the Malpais Borderlands: Conference Summary #RMRS-P-10, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

———. 1999b. Surgery on rattlesnakes in the field for implantation of transmitters. Sonoran Herpetol. 12:26–28.

HARE, T. A., AND J. T. MCNALLY. 1997. Evaluation of a rattlesnake translocation program in the Tucson, Arizona area. Sonoran Herpetol. 10:26–31.

HEATWOLE, H. 1977. Habitat selection in reptiles. Pp. 137–155 *In* C. Gans and F. H. Pough (Eds.), Biology of the Reptilia, Vol. 7, Academic Press, New York.

Hein, E. W., and S. J. Whitaker. 1997. Homing in eastern fence lizard (*Sceloporus undulatus*) following short distance translocations. Great Basin Nat. 57: 348–351.

Jacobson, E. R., and J. M. Gaskin. 1992. Paramyxovirus infection of viperid snakes. Pp. 415–419 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

Jemison, S. C., L. A. Bishop, P. G. May, and T. M. Farrell. 1995. The impact of PIT-tags on growth and movement of the rattlesnake, *Sistrurus miliarius*. J. Herpetol. 29: 129–132.

Jones, M. L., N. E. Mathews, and W. F. Porter. 1997. Influence of social organization on dispersal and survival of translocated female white-tailed deer. Wildl. Soc. Bull. 25:272–278.

King, M. B., and D. Duvall. 1990. Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging, and sex differences. Anim. Behav. 39:924–935.

———, D. McCarron, D. Duvall, G. Baxter, and W. Gern. 1983. Group avoidance of conspecific but not interspecific chemical cues by prairie rattlesnakes (*Crotalus viridis*). J. Herpetol. 17:196–198.

Klauber, L.M. 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind, 2 Vols., 2nd ed. University of California Press, Berkeley and Los Angeles.

Landreth, H. F. 1973. Orientation and behavior of the rattlesnake, *Crotalus atrox*. Copeia 1973:26–31.

Lawson, P. A. 1991. Movement Patterns and Orientation Mechanisms in Garter Snakes. Unpublished Ph.D. dissertation, University of Victoria, Canada.

Lloyd, B. D., and R. G. Powlesland. 1994. The decline of kakapo (*Strigops habroptilus*) and attempts at conservation by translocation. Biol. Conserv. 69:74–85.

Lunger, P. D., and H. F. Clark. 1979. Morphogenesis of fer-de-lance virus (FDLV) cultured at sub- (23°C) and supra- (36°C) optimal cell growth temperatures. J. Comp. Pathol. 89:281–291.

Macartney, J. M., P. T. Gregory, and K. W. Larsen. 1988. A tabular survey of data on movements and home ranges of snakes. J. Herpetol. 22:61–73.

MacMillan, S. 1995. Restoration of an extirpated red-sided garter snake *(Thamnophis sirtalis parietalis*) population in the interlake region of Manitoba, Canada. Biol. Conserv. 72:13–16.

Marcus, L. C. 1971. Infectious diseases of reptiles. J. Amer. Vet. Med. Assn. 159:1629–1631.

Martin, W. H. 1992. Phenology of the timber rattlesnake (*Crotalus horridus*) in an unglaciated section of the Appalachian Mountains. Pp. 259–278 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

May, P., T. Farrell, S. Heulett, M. Pilgrim, L. Bishop, D. Spence, A. Rabatsky, M. Campbell, Ayerigg, and W. Richardson. 1996. Seasonal abundance and activity of a rattlesnake (*Sistrurus miliarius barbouri*) in central Florida. Copeia 1996:389–401.

Minckley, W. L., and D. E. Brown. 1994. Tropical-subtropical wetlands. Pp. 268–287 *In* D. E. Brown (Ed.), Biotic Communities of the Southwestern United States and Mexico. University of Utah Press, Salt Lake City.

Moorbeck, J. 1998. Reptile translocation: an open discussion via e-mail. Sonoran Herpetol. 11:62–67.

Moore, R. G. 1978. Seasonal and daily activity patterns and thermoregulation in the southwestern speckled rattlesnake (*Crotalus mitchellii pyrrhus*) and the Colorado Desert sidewinder (*Crotalus cerastes laterorepens*). Copeia 1978:439–442.

Moriarity, J. J., and M. Linck. 1995. Reintroduction of bullsnakes into a recreated prairie. Pp. 42–56 *In* Proceedings of a Symposium on Minnesota's Amphibians and Reptiles: Their Conservation and Status. May 5–6, University of Minnesota, Minneapolis.

Mosillo, M., E. J. Heske, and J. Thompson. 1999. Survival and movements of translocated raccoons in northcentral Illinois. J. Widl. Mgmt. 63:278–286.

National Oceanic and Atmospheric Administration. 1996. Annual Summary of Climatic Data for Arizona, 1996. National Climatic Data Center, U. S. Department of Commerce.

National Park Service. 1980. United States Codes: Department of the Interior: National Park Service Organic Act. Title 16, Subchapter 1.

Neter, J., W. Wasserman, and M. K. Kutner. 1990. Applied Linear Statistical Methods, 3rd ed., Richard D. Irwin, Inc., Burr Ridge, Illinois.

Newcomer, R., D. Taylor, and S. Guttman. 1974. Celestial orientation in two species of water snakes (*Natrix sipedon* and *Regina septemvittata*). Herpetologica 30:194–200.

Nowak, E. M. 1998. Effects and Effectiveness of Rattlesnake Relocation at Montezuma Castle National Monument, Arizona. Unpublished M.S. thesis, Northern Arizona University, Flagstaff.

Odum, R. A., and M. J. Goode. 1994. The species survival plan for *Crotalus durissus unicolor*: a multifaceted approach to conservation of an insular rattlesnake. Pp. 363–368 *In* J. B. Murphy, K. Adler, and J. T. Collins (Eds.), Captive Management and Conservation of Amphibians and Reptiles. Society for the Study of Amphibians and Reptiles, Contrib. Herpetol. 11, Ithaca, New York.

Otsfeld, R. S., and R. H. Manson. 1996. Long-distance homing in meadow voles, *Microtus pennsylvanicus*. J. Mammal. 77:870–873.

Parent, C., and P. J. Weatherhead. 2000. Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia 125:170–178.

Parker, W. S., and W. S. Brown. 1980. Comparative Ecology of Two Colubrid Snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in Northern Utah. Milwaukee Publ. Mus. Pub. Biol. Geol. 7:1–104.

Perry-Richardson, J., and C. Ivanyi. 1992. Preliminary analysis of a study on the free-ranging rattlesnakes on Arizona-Sonora Desert Museum grounds. Appendix I *In* AAZPA 1992 Reg. Proc.

Peterson, C. R., A. R. Gibson, and M. E. Dorcas. 1993. Snake thermal ecology: the causes and consequences of body temperature. Pp. 241–314 *In* R. A. Seigel and J. T. Collins (Eds.), Snakes: Ecology and Behavior, McGraw-Hill, New York.

Platenberg, R. J., and R. A. Griffiths. 1999. Translocation of slow-worms (*Anguis fragilis*) as a mitigation strategy: a case study from S. E. England. Biol. Conserv. 90:125–132.

Prior, K. A. and P. J. Weatherhead. 1994. Response of free-ranging eastern massasauga rattlesnakes to human disturbance. J. Herpetol. 28:255–257.

Reinert, H. K. 1991. Translocations as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. Herpetologica 47:357–363.

———. 1992. Radiotelemetric field studies of pitvipers: data acquisition and analysis. Pp. 185–198 *In* J. A. Campbell and E. D. Brodie, Jr., (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

———. 1993. Habitat selection in snakes. Pp. 201–240 *In* R. A. Seigel and J. T. Collins (Eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York.

———, and R. R. Rupert. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus.* J. Herpetol. 33:45–61.

———, and R. T. Zappolorti. 1988a. Timber rattlesnakes (*Crotalus horridus*) of the Pine Barrens: their movement patterns and habitat preference. Copeia 1988:964–978.

———, and ———. 1988b. Field observations of the association of adult and neonatal timber rattlesnakes, *Crotalus horridus*, with possible evidence for conspecific trailing. Copeia 1988:1057–1059.

Rideout, D. L. 1993. Managing human population impacts on wildlife in a rapidly urbanizing area: a case study of the city of Carlsbad, California. Trans. North Amer. Wildl. and Nat. Res. Conf. 8:158–164.

Rodda, G. H., Y. Sawai, D. Chizar, and T. Tanaka. 1999. Snake management. Pp. 1–23 *In* G. H. Rodda, Y. Sawai, D. Chizar, and T. Tanaka (Eds.), Problem Snake Management: The Habu and the Brown Treesnake. Cornell University Press, Ithaca, New York.

Rosen, P. C., and C. H. Lowe. 1994. Highway mortality of snakes in the Sonoran Desert of southern Arizona. Biol. Conserv. 68:143–148.

Santana-Bendix, M. A. 1994. Movements, Activity Patterns, and Habitat Use of *Boiga irregularis* (Colubridae), an introduced predator in the island of Guam. Unpublished M.S. thesis. University of Arizona, Tucson.

Sealy, J. 1997. Short-distance translocations of timber rattlesnakes in a North Carolina state park: a successful conservation and management program. Sonoran Herpetol. 10:94–99.

Secor, S. 1994. Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes*. Copeia 1994:631–645.

Seigel, R. A. 1986. Ecology and conservation of an endangered rattlesnake, *Sistrurus catenatus*, in Missouri, U. S. Biol. Conserv. 35:333–346.

Sexton, O. J., P. Jacobson, and J. E. Bramble. 1992. Geographic variation in some activities associated with hibernation in nearctic pitvipers. Pp. 337–346 *In* J. A. Campbell and E. D. Brodie (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

Shine, R. 1993. Sexual dimorphism in snakes. Pp. 49–86 *In* R. A. Seigel and J. T. Collins (Eds.), Snakes: Ecology and Behavior. Mc-Graw Hill, New York.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: The Principles and Practice of Statistics in Biological Research, 2nd ed. W. H. Freeman & Co., New York.

Stephenson, B. R., and G. R. Pisani. 1991. Notes on early spring parasites and pathologies of Oklahoma *Crotalus atrox*. Herpetol. Rev. 22:88–90.

Turner, R. M., and D. E. Brown. 1994. Tropical-subtropical desertland. Pp. 180-221 *In* D. E. Brown (Ed.), Biotic Communities of the Southwestern United States and Mexico. University of Utah Press, Salt Lake City.

Van Vuren, D., A. J. Kuenzi, W. E. Loredo, A. L. Leider, and M. L. Morrison. 1997. Translocation as a nonlethal alternative for managing California ground squirrels. J. Wildl. Mgmt. 61:351–358.

Weatherhead, P. J., and K. A. Prior. 1992. Preliminary observations of habitat use and movements of the eastern massasauga rattlesnake (*Sistrurus c. catenatus*). J. Herpetol. 26:447–452.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-tracking Data. Academic Press, San Diego.

Whiting, M. J. 1997. Translocation of non-threatened species for ‘humanitarian’ reasons: what are the conservation risks? S. African J. Sci. 93:217–218.

Wilson, E. O. 1996. In Search of Nature. Island Press, Washington, D.C.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conserv. Biol. 10:1142–1154.