Spatial ecology, habitat use, and survivorship of resident and translocated red diamond rattlesnakes (Crotalus ruber)

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5 authors, including:

Jean-Pierre Montagne
San Diego Zoo

Jeff Alfred Tracey
United States Geological Survey

Allison C. Alberts
San Diego Zoo

FINAL DRAFT

Spatial ecology, habitat use, and survivorship of resident and translocated Red Diamond Rattlesnakes (*Crotalus ruber*)

Tracey K. Brown[1, 2, 4], Jeffrey M. Lemm[2], Jean-Pierre Montagne[2], Jeff A. Tracey[3] and Allison C. Alberts[2]

[1] Department of Biological Sciences
California State University, San Marcos
San Marcos, CA 92096

[2] Conservation and Research for Endangered Species
Zoological Society of San Diego
15600 San Pasqual Valley Road
Escondido, CA 92027-7000

[3] Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523

[4] Corresponding Author email: traceyb@csusm.edu

ABSTRACT

Red Diamond Rattlesnakes (*Crotalus ruber*) have a very restricted range in the United States and are considered a species of special concern in California. Over a five year period (1999-2004), we used radio-telemetry to collect data on the movement ecology and habitat use of this little-studied species on protected coastal sage scrub land managed by the San Diego Zoo's Wild Animal Park. During the study we compared the movement patterns and survivorship of "Resident" snakes (N=11; 11,090 radio-days) to several *C. ruber* relocated by Park staff for safety purposes ("Relocates"; N=6; 3,858 radio-days). Among Resident snakes, activity range sizes varied greatly both between individuals, and between years within individuals. Male Resident activity ranges (minimum convex polygon) were typically triple the size of Resident females (2.80 ha vs. 0.88 non-gravid females or 0.76 ha gravid females), and Resident males moved nearly twice as far during an activity season (1.38 km, Resident males vs. 0.77 km, Resident females). Overall, Resident *C. ruber* have relatively restricted movements when compared to other similar-sized rattlesnakes, typically never occurring more than 300 m linear distance from their winter dens. Relocates used significantly more land (mean activity range size 5.86 ha), and had greater maximum per move distances and total distances traveled during the first year after relocation than did Residents for the same time period. Activity range sizes, annual distances moved, and mean movement speed decreased over time among short distance Relocates (n=3; translocated 97 to 314 m), yet was similar or increased among long distance Relocates (n=3; translocated 856 to 1090 m). Only short distance Relocates were found near (within 50 m) their original capture site at some point during the study (30 to 364 d). Unlike most previous studies of relocated rattlesnakes, there was no detectable difference in survivorship between Residents and Relocates. If translocation is necessary for nuisance rattlesnakes, we suggest only short-distance relocations; long-distance translocations may be a potential conservation tool for future repatriations of *C. ruber*. We highly recommend more education and public outreach to minimize the need for snake removal.

INTRODUCTION

Urbanization is arguably the greatest cause of species endangerment in the United States (US, Czech et al. 2000), and approximately 2.2 million acres of land are developed each year in the US (USDA 2001). The southwestern US has witnessed remarkable population growth over the last few decades, and the most populous state, California, is projected to reach nearly 55 million people by 2050. The Mediterranean-type climate, which attracts so many people to California, is also thought to be one of the reasons California ranks first among US states in biodiversity and species endemism (Stein 2002). The unfortunate combination of human population growth and species endemism in California has had severe consequences. In fact, 8 of the nation's 21 most endangered ecosystems reside partially or wholly in California, including the southern California coastal sage scrub ecotype, thought to have already declined by 90% (Noss and Peters 1995).

Among reptiles, more species are listed as threatened, endangered, or of special concern in California at the state or Federal level than in any other US state. One such species of special concern is the Red Diamond Rattlesnake (*Crotalus ruber*; California Department of Fish and Game 1994). The majority of the range of this species includes Baja California (peninsula and several associated islands), where individuals inhabit a broad array of habitats, absent only from much of the Colorado desert and the coniferous forests of the Sierra Juárez and San Pedro Mártir ranges (Grismer 2002). In California, the range of this species is much smaller, including only a few southwestern counties, largely south of the Transverse Ranges and from the coast to the edge of Colorado desert (Klauber 1997; Stebbins 2003; Beaman and Dugan 2006). This area is also occupied by over eight million people and consequently, over 20% of suitable habitat may already have been lost to development (Marlow 1988; Jennings and Hayes 1994). The extremely small range of *C. ruber* in California justifies its status as a state species of concern and its inclusion in the habitat conservation plans of San Diego and western Riverside counties.

Although *C. ruber* has been recognized as a sensitive species by planning agencies, there are still large gaps in our knowledge of this species. Much of the natural history data for this species has come from museum specimens, captive animals, and opportunistic field captures (Klauber 1997; Ernst 1999; Grismer 2002; Stebbins 2003; and in Beaman and Dugan 2006). Several studies have investigated the phylogenetics of the *C. ruber* group. Both Grismer et al. (1994) and Murphy et al. (1995) synonymized the Isla de Cedros *C. exsul* with the peninsular *C. ruber*, and the specific name *ruber* has been given precedence (Anonymous 2000). Grismer (1999) also elevated *C. e. lorenzoensis* to *C. lorenzoensis*. Two subspecies of *C. ruber* are often noted (Klauber 1997; Stebbins 2003) including the Northern Red Diamond Rattlesnake (*C. r. ruber*) and the Cape Red or San Lucan Diamond Rattlesnake (*C. r. lucasensis*); however, the support for these subspecies is tenuous (B. Hollingsworth, pers. comm.) and Grismer (2002) suggests considering them as pattern classes.

Very few studies of *C. ruber* ecology and distribution have been done, two of which are reported in this volume (see Dugan et al. and Halama et al.). Tracey (2000) and Tracey et al. (2005) developed nonlinear regression models for testing the effects of landscape structure on *C. ruber* home range and movement. Greenburg (2002) studied how the distribution of non-food resources such as mates and den sites affected movement of desert dwelling *C. ruber* along with *C. mitchellii*. Although these studies investigated movement, they focused largely on interactions between snakes and specific landscape features. A primary purpose of the present study was to gather long-term data on the habitat use and movement patterns of coastal *C. ruber*.

In addition to habitat loss, another consequence of urbanization is increased human-wildlife interactions and the need to manage species which are potentially dangerous to humans. If not killed outright, snakes are often captured for removal from human habitation by officials and the general public (Shine and Koenig 2001; Butler et al. 2005b). While many snakes are destroyed, some captured snakes are translocated to new areas deemed “suitable” by rescuers (Shine and Koenig 2001). Translocation (defined here as the movement of individual animals by humans from one part of their range to another, and synonymous with “relocation”) of any species is outwardly appealing to the public, but the near universal message from studies of such activities has been one of caution (Griffith et al. 1989; Fischer and Lindenmayer 2000). Whether used as a *conservation* tool (i.e. repatriations, restocking, reintroductions of entire populations) or as a *management* tool (i.e. relocations of individual animals away from human establishments), translocation success is complex and depends on a variety of variables that may not be known (Burke 1991; Wolf et al. 1996; 1998).

Translocation efforts of non-venomous reptiles have largely involved repatriations, and the success of these studies have been alternatively judged negative (reviewed by Dodd and Seigel 1991), positive (Tuberville et al. 2005) or undetermined (Macmillan 1995; Platenberg and Griffiths 1999; Towns and Ferreira 2001). Venomous reptile translocations have similarly reported mixed results, with many species demonstrating aberrant movement patterns post-release and high or increased mortality rates (Hare and McNally 1997; Sealy 1997; Reinert and Rupert 1999; Plummer and Mills 2000; Hardy et al. 2001; Nowak et al. 2002; Sealy 2002; King et al. 2004; Sullivan et al. 2004; Butler et al. 2005b). Above all, whether individuals were moved short (within an animal's previous activity area) or long (outside its activity area) distances appears critical to the final outcome of the translocation (Hardy et al. 2001; Nowak et al. 2002; Sealy 2002; Sullivan et al. 2004).

During the course of our study on resident *C. ruber* ecology, we were presented with the opportunity to study the effects of translocation on movement and survivorship. The resident study population was located on the lands managed as a natural reserve by the San Diego Zoo's Wild Animal Park. Over half of the Wild Animal Park's (Park) 1,800 acres is protected native habitat (San Diego Multiple Species Conservation Program) supports a healthy population of *C. ruber*. Over 1.25 million people visit the Park grounds annually, and its collection includes over 3,500 animals. As the public areas and animal enclosures are surrounded by native habitat, encounters by visitors, park staff, and captive animals with rattlesnakes are not uncommon. In response to safety concerns, Park staff have historically translocated any of the three rattlesnake species found in the developed portion of the Park into the adjoining reserve lands. We used these occasions to study the effects translocation on *C. ruber* movement and survivorship.

The need for long-term data on life-history, habitat use and movement patterns has been identified as a research priority for the conservation of snakes (Dodd 1993), and such information has been useful in the development of management plans for several species (Timber Rattlesnakes, *C. horridus*, Brown 1993; Northern Pine Snakes, *Pituophis melanoleucus melanoleucus*, Zappalorti and Burger 1985; Eastern

Diamondback Rattlesnakes, *C. adamanteus*, Timmerman and Martin 2003). In the present study, our goal is to increase the small body of knowledge regarding *C. ruber* and help inform decisions on the management of this sensitive species.

MATERIALS AND METHODS

Study Site

From late 1999 through early 2004 we studied *C. ruber* at the Park. The dominant vegetation in this area is coastal sage scrub (composed mostly of *Salvia mellifera* and *S. apiana*, *Eriogonum fasciculatum*, *Artemisia californica*, and *Malosma* (*Rhus) laurina*) along with large areas of prickly pear cactus (*Opuntia* sp.). Large granitic boulders are common and much of the terrain is steep; several unpaved roads intersect the study area. There are 16 documented snake species in the study area, including two congeners of *C. ruber*, the Speckled Rattlesnake (*C. mitchelli*) and the Southern Pacific Rattlesnake (*C. (viridis) helleri*).

Although temperatures at the Park can fall below freezing (30-year low is -5.6 C), most winter days are mild, and the 30-year average monthly high temperature is above 21 C (70 F) in all months (Western Regional Climate Center, 1979-2005 data). The 30-year average annual precipitation for the Park is 35.5 cm, and most rainfall occurs during the cooler winter months.

Telemetry

Transmitters (model SI-2T, Holohil Inc. Canada) weighed approximately 9 g (all transmittered snakes were > 500 g, range 510 to 1,380 g) and were rated to last 12 months at 35 C. Because the transmitters were temperature-sensitive, the actual transmitter lifespan was typically 16 to 18 months (due to reduced pulse rates during winter). During 2003, a batch of defective transmitter batteries that were supplied to Holohil by another vendor (pers. comm.) resulted in the premature failure of several transmitters and the loss of four study animals. All surgeries for transmitter implantation were done at the San Diego Zoo by veterinary staff. Transmitter implantation methods were adapted from Reinert (1992). Snakes were typically released within 48 hours of surgery. When possible, transmitters were removed at the end of each animal's study period, after which snakes were treated for any bacterial infections detected by pathology cultures and released. Snakes followed over several years had up to three transmitters during the study, and surgery dates were timed to avoid any recovery complications due to winter brumation (Rudolph et al. 1998). All transmittered snakes had non-toxic red paint injected into the basal rattle to facilitate identification in the field, and had passive integrated transponder (PIT) tags (ID100, Trovan Ltd., United Kingdom) injected for long-term identification.

Snakes were located one to three times weekly while active, and bi-weekly during winter brumation; locations were recorded with a GeoExplorer 3c GPS unit (Trimble Navigation Ltd., Sunnyvale, CA). At each sighting we recorded: snake posture (e.g. coiled, stretched out, moving), habitat type (i.e. "associated with rocks" which included in, under, adjacent to, or on rocks; in "vegetation-only" habitat with no rocks within 5 m; in or adjacent to "*Neotoma* sp. nest"; on "open soil"; "in burrow" or "other structure"), vegetation type (i.e., plant species or types seen at each location), relative percent cover (determined as amount of vegetative (shade) cover directly over snake: 0-25%, 26-50%, 51-75%, 76-100%), indications of feeding or reproductive activity (e.g., distended bodies, courtship), external body temperature (used Raynger infrared thermometer, Raytek Santa Cruz, CA), and transmitter pulse rate.

Relocations

During our study, several rattlesnakes were captured by Park staff for relocation away from public trails and animal enclosures. Six of these snakes (all captured in animal enclosures) were *C. ruber* large enough to receive transmitters (> 500 g); each snake was randomly assigned to be translocated either a short or long distance. We released short distance translocates (SDT) in undisturbed native habitat closest to their original capture sites, which resulted in relocation distances of 97, 149, and 340 m. Long distance translocates (LDT) were released at a location historically used by Park staff for nuisance snake release resulting in relocation distances of 856, 893 and 1,090 m. Previous studies have defined LDT as those relocations that move rattlesnakes well beyond their familiar or usual home ranges (Hardy et al. 2001; Sealy 2002), or more than twice the straight-line distance between any two locations in a year (Nowak et al.

2002). In the two years prior to the commencement of our translocation study, the greatest straight-line distance between any two locations of an individual non-translocated (Resident) snake was 716 m. As this value (716 m) was straddled by our SDT (≤ 340 m) and LDT (≥ 856 m) translocation distances, we felt our SDT/LDT designations were appropriate for this species. All translocations occurred late-afternoon during summer (Jun.-Aug.), and the relocated snakes (Relocates) were released under large rocks.

Analyses

GPS locations were post-processed to one meter accuracy using Pathfinder Office v. 2.8 (Trimble Navigation Ltd., Sunnyvale CA). We used the Animal Movement Extension v2.0 (AME, Hooge and Eichenlaub 1997) of ArcView v.3.3 (ESRI, Redlands, CA) to calculate land use and several movement parameters. Because several of the snakes in this study were translocated animals, we follow Hare and McNally (1997) and use the increasingly common term "activity range" in place of the more traditional term "home range" to describe the amount of land covered by the snakes during a specific period. Activity ranges were estimated as 100% minimum convex polygons. For comparison, we also calculated 95% and 50% fixed kernel home ranges computing the smoothing factor via least-squares cross validation (Seaman and Powell 1996). To determine the minimum acceptable sample size for calculating the activity ranges, we bootstrapped 10 randomly selected activity ranges 100 times each and assessed the effects of sample size on activity range size results visually.

Because the snakes were typically inactive during December and January, we used the calendar year for between-year comparisons. Movements were estimated as the straight-line distance between successive locations, likely underestimating true movement distances by half (Secor 1994; Reed and Douglas 2002); however, this index of movement is comparable to other authors. Speed (mean meters per day) was estimated by the more commonly used method (Diffendorfer et al. 2005) of dividing the total distance traveled (sum of all straight-line distances) by the number of days over which the travel occurred. To assess the maximum distance snakes roamed away from their over-winter locations each year, we measured the straight-line distance from an individual's winter den to the furthest location away from the den at which it was found the following year (hereafter referred to “ranging”). Overall tortuosity (sinuosity) of the snakes’ movement paths was assessed by calculating the fractal dimension (D) for each path of interest (Crist et al. 1992). Fractal D values typically range from 1.0, indicating highly linear movements, to 2.0, indicating extreme tortuosity. We used the program Fractal v. 4.0 (Nams 1996) to calculate the mean fractal D; paths of less than five moves were excluded. Tests for directionality of movements (homing) were done using Rayleigh’s z test for uniformity of angles (AME, Fisher 1993; Zar 1996).

Survival rates were calculated from the telemetry data using the Kaplan-Meier procedure (Pollack et al. 1989), which does not have the restrictive assumption of constant survival probability (Robertson and Westbrooke 2005). The time period for the survival calculations was the number of days a snake was known to survive, and the start date was the first date a snake moved in the field after release from surgery (deaths resulting from surgery complications, determined by necropsies, were excluded). The final date was recorded as 1) the date a snake was found dead in the field, or 2) the date a live snake was captured (appeared thin and sickly) but subsequently died in captivity, or 3) the date a live telemetered snake was captured for transmitter removal and release from the study, or 4) a censored final date, equivalent to the mid-point date between the last time the snake was tracked and the first time it was tracked and not found, for cases of early transmitter failure, unknown fate or failure to recapture (Miller and Johnson 1978). The number of days any snake was held in captivity for transmitter surgery or recovery were subtracted from the total days tracked. Survival calculations were performed using SPSS v. 13.0 (SPSS Inc. Chicago, Ill.) as detailed by Robertson and Westbrooke (2005), and the log-rank (Mantel-Cox) option in SPSS was used to test for differences in survival between Residents and Relocates.

If necessary, data were log-transformed to meet the statistical assumptions of normality and equality of variances. We used chi-square tests of independence to compare habitat use data between Residents and Relocates, and to assess any effects of month or sex on frequency of movement (tested as the percent of locations in each month in which a snake moved more than 5 m). The effects of sex, year, and status (Resident vs. Relocate) on activity range and other movement parameters were also assessed. Because not all snakes were tracked in all years, a true multivariate repeated-measures ANOVA (GLM) was not possible. Thus, data for Residents were first compared within years to test for any effects of sex before comparisons between years were made. The data from the Relocates were also compared within and between years, and between SDT and LDT snakes. For the translocated animals, movement data were also categorized into Year 1 (movements made from the initial release date until 12/31 of same year), Year 2 (1/1 to 12/31 of second year following release), and Year 3 (1/1 to 12/31 of third year following release). Because Year 1 data for the translocated snakes only represented approximately half of the activity season (Jun.-Dec.), any Resident comparisons to Year 1 data were limited to the same time period. SPSS v. 13.0 (SPSS Inc. Chicago, Ill.) and was used for these statistical analyses. Unless otherwise indicated, reported values represent means ± one standard deviation.

RESULTS

General

A total of 41 adult *C. ruber* were encountered during the five-year study period. Seventeen snakes (mean body mass 0.80 ± 0.28 kg) provided telemetry data for various periods between late 1999 and 2004 (Table 1), including 11 Residents (animal I.D. begins with "C") and 6 Relocates (animal I.D. begins with "R"). Although we were not actively searching for new snakes, at least 24 other adult *C. ruber* were seen during the study, typically during the breeding season, in association with transmittered snakes. The entire area over which the 41 snakes were found was approximately 65 hectares (Fig. 1), giving a minimum apparent density estimate of 0.63 *C. ruber* per hectare, and the greatest distance between any two tracked snakes was 2.1 km. The actual density is likely higher, as another researcher found 31 *C. ruber* in 2005 (general vicinity of the present study area) during six months of active searching (R. Zacariotti, pers. com.).

Seasonal Activity and Habitat Associations

Residents typically emerged from their over-winter locations in late February. One snake made her first major move (> 5 m) at the end of January in each of two years, while others remained inactive until mid-April. Although emergence dates varied both within and between individuals, and Park temperatures were fairly consistent between years, the earliest per-individual emergence dates occurred in 2003 after a prolonged heat wave in January. Evidence of feeding (distended bodies, recently killed rodent nearby) was seen February through October.

At least 7 of the 11 Residents over-wintered communally (sometimes with up to seven other *C. ruber*) in narrow rock crevices of large granitic boulder outcrops. Most snakes used the same den site each year, and a few changed locations every year. One snake even used a burrow under a hay bale for brumation. Residents consistently entered over-winter locations during November of each year. Four snakes were not visible during winter because they were located under large cacti or boulders. Dates of entrance and emergence from brumation in Relocates were similar to the Residents. Detailed data on den characteristics and availability are still being analyzed and will be published elsewhere.

Examination of the habitat and vegetation data for each snake location confirmed our field impressions that rocks and cacti are important habitat features for *C. ruber*. Among Residents, 57% of unique locations had some degree of association with rock outcrops (snakes were either in, under, or adjacent to large boulders or clusters). About 28% of Resident locations were in vegetation-only habitat (no rocks within 5 m), and the remaining locations included woodrat nests (*Neotoma* sp.; 8%), burrows (5%), open soil (1%), or were under man-made structures (1%). In contrast, the majority (53%) of unique locations of Relocates were in vegetation-only, and only 25% of locations were associated with rocks even though the Relocates often occurred in the same areas as Residents. Burrows, open soil, and *Neotoma* nests made up 12, 5, and 4% of Relocate locations respectively. Differences in habitat use categories between Residents and Relocates were significant (X^2=80.5; *df*=4; P<0.0001).

In those habitat type locations categorized as vegetation-only, both prickly-pear cactus (*Opuntia* sp.) and small-medium shrubs (e.g., California sagebrush-*Artemisia californica*, Coyote Brush-*Baccharis pilularis*) were common (each 28% of locations), followed by annual plants-grass (19%), large shrubs (e.g. Laurel Sumac-*Malosma laurina*; 15%), and California Buckwheat (*Eriogonum fasiculatum*; 7%). There were no apparent differences between the plants used by Residents and Relocates in vegetation-only habitat locations, nor between SDT snakes and LDT snakes.

Activity Ranges and Movement

Residents. – Movement behavior of Residents varied greatly within and among individuals, and between years (Table 2; Fig. 2, left panels). As a result of high individual variation, no consistent pattern was attributable to year. Despite large annual differences in movement patterns within individuals, most displayed strong site fidelity and repeatedly used the same locations in different years for foraging and denning.

As expected, Resident females had significantly different ARS from Resident males. There was a near seven-fold difference between the largest male mean activity range size (ARS) and the smallest female ARS (Table 2); overall mean male ARS was approximately triple the size of the overall mean female ARS (see Table 2 for statistics). Between years, Resident females tended to have very similar ARS sizes, while more inter-year variation was seen among the Resident males (Fig. 2, top left panel). Although several Resident females had smaller ARS when gravid (mean gravid ARS 0.76 ± 0.41 ha vs. 0.89 ± 0.38 ha), this decrease in ARS was not statistically significant (paired t-test; df=4; P=0.131). The ARS size was not correlated to initial body mass or length for either sex.

Our attempts at calculating kernel home ranges (KHR) were complicated by the fact that KHR are very sensitive to sample size (Seaman et al. 1999). Most calculated 95% KHRs were many times greater than ARS, thus, we did not have much confidence in the 50% KHR estimates. However, an estimate of "core" habitat use was derived from a comparison of the overlap between years of all annual ARS for an individual (see Fig. 3 for example). When compared to the pooled ARS (i.e. represents outline of all annual ARS combined for an individual), the mean area contained within every annual ARS represented 22.9 ± 12.4 percent (0.67 ± 0.66 ha) of the pooled ARS. Thus, of all the area used by each snake throughout the study, nearly one-quarter was used every year (Fig. 3). The core area typically included the brumation site of an individual if they repeatedly used the same over-winter location.

Although related, a snake that moved further in a given year did not necessarily demonstrate a proportional increase in ARS size (Fig.2; compare top and bottom panels). For example, Resident male C19 traveled 126% more total distance in 2003 than he did in 2000, yet his ARS only increased 14% between those years (Fig. 2).

Resident males typically traveled significantly greater distances during a year than did Resident females (Table 2), and the greatest annual distance moved in any year by a Resident was 2.4 km (Resident male C19). Males also moved further than females each time they moved (see Table 2 for statistics). Neither sex ranged very far from their over-winter locations in each year; the mean maximum ranging distance between a den and the furthest location away from that den a snake was found during the following year was only 159 ± 74.3 m (range 77 to 304 m). Ranging distance was highly consistent within individuals and between years (average SD between years per individual was 37 m), although most females exhibited reduced ranging behavior when gravid.

Despite the difference in movement distances between the sexes, there was no significant difference in the frequency of movement between Resident males and non-gravid Resident females during the activity season (Feb.-Nov.; Fig. 4A,B). Both sexes frequently moved during the months when we witnessed courtship and mating (Apr., May). Most movements took place during the late spring and summer months (Fig. 4); once in their hibernacula, Resident males did not move Dec.-Jan. (Fig. 4A). In contrast, several Resident females emerged in Jan. to move to a new location where they would remain for several weeks (Fig. 4B). The overall frequency of movement of gravid Resident females was significantly lower than for males or non-gravid females (X^2= 65.5 between gravid females and males; X^2 = 59.0 between gravid and non-gravid females; df=9 and $P<0.001$ for both). Gravid females demonstrated especially infrequent movement during June through mid-September, and resumed moving after parturition in September (Fig. 4C).

Relocates. – We relocated four snakes in 2001, and two additional snakes in 2002; most snakes were followed for two years, although R28 was followed for three (Table 1). Only two of the six relocated snakes were females. It was difficult to determine if there was any effect of sex on the movements of the Relocates, as the two relocated females routinely demonstrated some of the largest and smallest movement parameters (Table 3; Fig. 2), and individual variation was high.

During the first month after translocation, two SDT snakes (R26, R34) returned to within 50 m of their original capture location (Fig. 5A, B). Neither snake returned to its capture or release location during the remainder of the study. In contrast, the third SDT (R27) did not immediately return to his original capture location. However, approximately one year (335 days) after his original release, R27 was repeatedly found him within 50 m of the original capture site (Fig. 5C). No directional bias was detected in the LDT data for any individual, suggesting a lack of homing behavior (see Fig. 5D-F); the nearest distance any of the LDT snakes came to their original capture location was 690 m. One LDT (R25) did make several long distance moves in the direction of her original capture location during the second year she was followed (Fig. 5D).

Overall, there was a high degree of variability in the response to relocation (Fig. 2). In the activity season following release (Year 1), there was no detectable effect of translocation distance (i.e. SDT vs. LDT) on ARS, total distance moved, mean distance per move, or mean daily speed among Relocates (Table 3). The largest Year 1 movements were made by male R26, a SDT who was translocated only 340 m. In the first five months following translocation, R26 covered at least 2.2 km, had a ARS more than twice as large as any other Year 1 translocated snake, and also had the highest mean distance per move and daily speed (Table 3). In contrast, the shortest total distance, shortest mean distance, and slowest speed values were calculated for male R33, an LDT who was moved 856 m.

Initial comparisons between Year 1 and Year 2 movement suggested contrasting responses by SDT and LDT snakes (Table 3, Fig. 2). For example, both R26 and R33 seemed to reverse their movement behavior during Year 2; the movement parameters of SDT R26 generally declined, while all values for LDT R33 increased greatly (Table 3). When Year 1 data for all snakes were compared with Year 2 data (Table 3), it appeared that ARS, mean distance per move, and mean daily speeds all declined for SDT in Year 2. Total distance moved appeared to increase for all snakes in Year 2, and ARS increased among LDT. However, it is important to note that Year 2 data represented complete activity seasons (emergence until following winter, ~ 9 months), while Year 1 data typically only encompassed five months. When Year 2 data were censored to include only the same months as Year 1 data (i.e. Jun.-Dec.), no significant differences were found between Year 1 and Year 2 movement parameters.

SDT snakes used very similar areas between the study years. Both movement path and ARS overlap appeared greater among SDTs than among LDTs (Fig. 5 A-F). The proportions of the Year 1 ARS covered by Year 2 ARS were 23, 37, and 66% among the three SDTs, and only 5, 10, and 29% among the three LDTs; the difference in these values approached significance (one-tailed t=2.05; *df*=4; P=0.055). Similar to Residents, the three SDTs all moved quite quickly to over-winter locations in November of each year, and SDT R26 used the same den twice (Fig. 5A).

Among the LDTs, R25 continued to move (did not den) during the single winter we followed her and was visible on most days (Fig. 5D). In contrast, LDT R28 successfully located a large communal den his first winter in mid-November approximately 320 m from his release point (Fig. 5E). During Year 2 he left the communal den, moved throughout a different area from Year 1 (only 10% overlap of ranges), and returned to the same den in November. LDT R33 spent December of Year 1 under a large cactus. In early Year 2, R33 moved at least 992 m (Fig. 5F) over a one month period to an area several other *C. ruber* were known to inhabit (including Residents C13, C15, C17, C18, and Relocate R28). In fact, R33 was found several times within 5 to 30 m of locations previously used by LDT R28 in the same year and in December of Year 2, R33 was found in the same communal den as R28.

As mentioned previously, LDT R28 was the only snake we were able to follow a third year. Although he traveled his greatest total distance (2.1 km) and he had his largest ARS (5.4 ha) in Year 3, his Year 3 ARS included 81% of his Year 1 range and 72% of his Year 2 range, and he used the same communal den for three consecutive winters.

Resident vs. Relocates – During the first year we translocated snakes (2001), the four relocates moved further, faster, in greater segments, and had larger overall ARS than did Residents for the same time period (Jun.-Dec.; gravid Residents excluded; N=4 for each group; all P values < 0.03). Although these early comparisons were significant, statistical significance of the greater movements demonstrated by the Relocates hinged on whether the comparison Resident group included females. When compared to male-only mean Resident values (all years combined, data from Table 3), Relocates (Year 1 and Year 2 combined) had only marginally larger ARS (t = 1.76; P = 0.055). However, when females were included in the Resident group, ARS, total distance moved, mean distance per move, and mean daily speed were all significantly less than for Relocates (all P's < 0.01).

Many of the Relocated ARS were larger in total area than any ARS calculated for Residents (Fig. 2, top panels). The greatest straight-line distance between any two location points in a given year (primary axis) was significantly longer for Relocates than for Residents (males only or females and males; t-tests, both $P < 0.03$). Thus, the typical Relocate ARS was both larger and longer (relatively more elliptical) than Resident ARS. Despite having larger ARS, Relocates rarely traveled more (total distance) than Residents (Fig. 2, bottom panels).

Tortuosity Comparisons

Both the lowest (1.086) and highest (1.405) fractal D values were held by Residents (mean 1.202 ± 0.076), with intermediate values for Relocates (Year 1 mean 1.207 ± 0.107, Year 2 mean 1.15 ± 0.044). Most fractal D values decreased between Year 1 and Year 2 for Relocates, suggesting more linear movements in the year following translocation; however, this difference was not significant (paired t-test; *df*=4; P=0.128). A priori we expected fractal D values of Relocates could be either higher (if snakes were exhibiting meandering movements in an attempt to orient) or lower (if snakes were exhibiting linear movements in an attempt to return to their original capture areas) than fractal D values for Residents. The Year 1 fractal D values for Relocates tended to be higher than the fractal D values for Residents for the corresponding time period (i.e. Jun.-Dec.); this difference was significant for a one-tailed (*df*=6; P=0.03), but not two-tailed (*df*=6; P=0.07), t-test.

Reproduction

Courtship and copulations were seen April-May, gestational denning June-September, and all recorded births occurred in September. Although no Relocate female is thought to have been reproductively active, several of the Resident females gave birth during the study period (no births occurred in 2000). Three (C14, C15, C18) Resident females are believed to have given birth in September 2001. Two of these females were seen associating and copulating with male snakes in April 2001, and all three had very limited movements from late May until September when either neonates were seen or neonate sheds were found. Both C15 and C18 had annually overlapping activity ranges and were found together under a single large rock throughout June 2001. In 2002, C30 was seen with a male in her winter den in late March and her late summer movements were restricted to two dens from May through September when neonate sheds were found. Although Resident males were observed mating with more than one female per season, no Resident female was seen mating with more than a single male in any year. Three of the four male Relocates (one SDT, two LDT) were observed courting or mating during the study.

Survival

The 11 Residents and 6 Relocates were tracked for a total of 11,090 and 3,858 radio-days, respectively (Table 1), and five deaths are known to have occurred during the study. Three of these deaths (one Resident, two Relocates) occurred soon (1, 2 and 30 days) after surgery for transmitter renewal. Because both Residents and Relocates died, and based upon necropsy results (suggested infection at surgical site), we believe these deaths are attributable surgery complications. The only possible depredated rattlesnake was Resident (C15), found decapitated in the field in 2001. One LDT (R25) was captured at the end of 2002 because she appeared severely underweight; she died the following day in captivity and necropsy resulted suggested long-term disease. Five snakes were lost prematurely when their transmitters failed early as a result of bad batteries, and we were not able to recapture two snakes before their transmitters stopped on schedule.

The only snake of unknown fate was Resident female C18; her transmitter signal ceased after October 2001, only eight months after implantation. Because C18's transmitter was not from the defective batch, it is possible she was depredated to the extent that the transmitter was damaged or removed from the study area (we could typically hear signals from over 1 km away). Assuming two snakes died in the field (the decapitated Resident and Relocate R25), and C18's transmitter failed (i.e., she was considered alive and her study date censored when last heard), the mean survival time for all snakes was 1,262 ± 82 (SE) days, 1,310 ± 73 (SE) days for Residents, and 799 ± 64 (SE) days for Relocates. The shorter survival time for Relocates largely results from the way survival time is calculated by the Kaplan-Meier procedure as the Relocates were brought into the study at later dates than Residents. If we assume C18 was depredated, the overall mean survival times decrease slightly to 1,208 ± 91 days for all snakes, and 1,240 ± 92 days for Residents. Regardless of C18's final status, no significant difference in survivorship between Residents and Relocates was detected.

DISCUSSION

Ecology of Residents

Seasonal Activity and Habitat Associations - The seasonal activity patterns of Residents were similar to many southern rattlesnake species (Klauber 1997). Although the snakes were largely inactive during the winter, they did appear to be responsive to short-term weather patterns. A two-week "heat-wave" triggered the early emergence of most of our study snakes in January 2003; Klauber (1997) similarly noted rattlesnakes sunning themselves in coastal southern California during "warm spells". When the weather in 2003 became relatively cool again during February, the snakes were largely inactive but did not return to their dens.

As mentioned previously, specific physical characteristics of the over-winter locations we observed are being published elsewhere; however, it is of interest to note the general den use of our study population differs markedly from the two other radio-telemetry studies of *C. ruber*. Whereas the majority of our study animals denned communally, all of the *C. ruber* Greenburg (2002) studied in the Colorado Desert over-wintered singly. Furthermore, although two of the *C. mitchellii* Greenburg followed showed high site fidelity by repeatedly using the same hibernacula, the distance between successive years' hibernacula for his *C. ruber* ranged from ~25 to 560 m. All but one Resident in our study followed for more than one winter returned to the exact same hibernacula at least twice, if not more often; some snakes alternated between two hibernacula (no more than 195 m apart) over three or four winters. Dugan et al. (this volume) followed male *C. ruber* over three years at a site that did not contain any rock outcrops, and the snakes also over-wintered singly under large *Opuntia* sp.. Greenburg (2002) attributed the individual denning behavior of desert *C. ruber* to temperate weather conditions; however, winter temperatures at the Park are similar to the desert yet the Park snakes denned communally. Klauber (1997) described 24 *C. ruber* that were blasted out of a rock crevice in San Diego County in 1932. Perhaps den sites are limited in certain areas, resulting in communal denning; alternatively, *C. ruber* may be quite variable in its denning behavior throughout its range.

There appears to be a strong correlation between *C. ruber*, stands of *Opuntia* cacti, and granitic boulders at our study site. Many previous authors report *C. ruber* to be most commonly associated with rocks and "brushy" or "scrub" habitat (Klauber 1997; Grismer 2002; Stebbins 2003). Nearly 60% of all snake sightings in this study involved rock outcrops of some sort, and 28% of the vegetation-only locations included small and medium shrubs. At the remaining vegetation-only locations, another 28% of the observations specifically involved *Opuntia* sp.. Large stands of cacti no doubt provide the snakes with protection from predators and may be good ambush sites for *Neotoma* sp. and other rodents frequently found there. *Neotoma* nests were common locations for the snakes, and were also typically found in or near cactus or Laurel Sumac. Beck (1995) similarly found *C. atrox* frequently used *Neotoma* nests associated with *Opuntia* as shelter. Utilizing cacti is not without cost; many of the snakes we observed had numerous spines attached around their mouths and along their bodies.

Despite the frequency of association with rocks and cacti, it is important to note that our habitat observations are indicative of habitat utilization rather than selection (Reinert 1993); our preliminary observations are included here primarily for informative purposes. Although habitat availability is often determined using GIS vegetation analyses, this information for the Park is simply not currently available at the resolution at which we observed the snakes moving. Admittedly, rocky habitat is common at the Park because the study site is located on the Peninsular Ranges Batholith, which is typified by numerous, large uplifted decomposing boulders (granodiorites, Sharp 1975). Although it appeared to us that the snakes at the Park were using rocks and cactus more frequently than they were available, *C. ruber* populations have been found in a variety of habitat types (Grismer 2002), including areas devoid of rocks (Dugan et al. this volume).

Movement – Compared to other large-bodied rattlesnakes, *C. ruber* has remarkably circumscribed movements. The mean ARS of both females (0.9 ha) and males (2.8 ha) were most similar to those reported for *C. pricei* (max. ♀ 0.8 ha; max. ♂ 2.3 ha; Prival et al. 2002), a species less than half the body size of *C. ruber*. The ARS size (in ha) for other large-bodied rattlesnakes are typically several times larger: *C. adamanteus* 46.5♀; 84.3♂, (Timmerman 1995); *C. atrox* 24.3, (Nowak et al. 2002); *C.*

horridus 41.9♀; 59.9♂ (Reinert and Rupert 1999); *C. viridis* 6.5♀; 12.1♂ (reported in Macartney et al. 1988); *C. viridis abyssus* 5.2♀; 15.8♂ (Reed and Douglas 2002). Although the ARS for three sympatric desert species studied by Beck (1995) were relatively smaller than many other rattlesnake species, the reported values (*C. atrox* 5.4 ha; *C. molossus* 3.5 ha; *C. tigris* 3.5 ha), are still larger than those we estimated for the larger bodied *C. ruber*.

Both the mean distance moved per day and per year by Residents in this study (♀: 3.6 m d^{-1}, 0.8 km; ♂: 6.8 m d^{-1}, 1.4 km) were also markedly less than for many rattlesnake species (Macartney et al. 1988; King and Duvall 1990). Even most of the smallest mean distance values reported by Beck (32 m d^{-1}, 9.3 km for *C. tigris*; 1995) and Reed and Douglas (26 m d^{-1} for *C. viridis abyssus*; 2002) were several times larger than our values for male *C. ruber*. Movement distances of *C. ruber* were again similar to those for *C. pricei* (Prival et al. 2002).

Although there is little, if any, sexual dimorphism in body size or coloration of *C. ruber*, we documented significant differences in movement behavior between male and female Residents. Similar differences between the sexes have been found for several *Crotalus* species (Macartney et al. 1988; Reinert and Rupert 1999; Reed and Douglas 2002; Ashton 2003). The larger movement distances and ARS sizes in Resident males seem to result from their tendency to move further each time they move, rather than moving more frequently. Interestingly, the frequency with which males moved did not appear to differ between spring (presumably when searching for mates) and late summer.

Resident ARS and distance values are remarkably similar to those found by Dugan et al. (this volume). In his study of male *C. ruber* in Riverside County, California, he found active season ARS of 0.34 to 4.5 ha and mean daily distances of 2.9 to 11.9 m d^{-1}. While our study site was almost entirely coastal sage scrub vegetation, his study location mostly contained grasslands, woodlands, and some coastal sage scrub. Large *Opuntia* are present at both sites; however, his site is completely devoid of the large, granitic boulders found at the Park. In contrast, Greenburg (2002) found desert dwelling *C. ruber* to have much larger ARS (5.85 ha ♀; 25.8 ha ♂) and mean annual movement distances (1.4 km ♀; 3.2 km ♂). His estimates of ARS appear to include all locations for an individual snake over his entire study period, which often spanned several years. Even if our data are recalculated to merge all annual ARS together for each Resident snake with multiple years' ARS, mean values (1.5 ha ♀; 5.3 ha ♂) remain substantially smaller.

We suspect much of the difference in the movement patterns between the *C. ruber* in our study and other *Crotalus* is because the study snakes never traveled very far from their winter dens. Unlike many other rattlesnake species that undertake long seasonal migrations (King and Duvall 1990; Klauber 1997), the entire activity season of a typical Resident *C. ruber* took place within a radius of 300 m of their over-winter location. Although the snakes rarely re-entered den sites during the year, they would often travel past or be found in close proximity to these locations. They did not display the "looping" behavior found in many other *Crotalus* species (Reinert and Rupert 1999). Instead, Residents extensively used a small area, with substantial overlap between years. The greatest distance a snake (C16) ventured was 680 m from a den (done one month after spring emergence), in 2003 during the fifth year he was followed. He appeared to be returning in August when his transmitter failed.

Even though the actual distances the Park snakes moved were small compared to other rattlesnakes, Residents were quite active, typically moving more than 50% of the time during the active season (compare unique vs. actual locations from Table 2 and Apr.-Oct. in Fig. 4). We did not sample prey availability during this study, however, given the limited movements of the snakes and the relatively high apparent density of this population, it is likely prey are abundant in the area. It is interesting to note that very few other rattlesnakes (*C. (viridis) helleri, C. mitchellii*) were seen during our field activities.

Reproduction – Similar to other southern species (Klauber 1997), Resident *C. ruber* females mated in spring and gave birth several months later (parturition for all females in this study occurred in September). These results confirm previous observations of spring-only mating in *C. ruber* (Aldridge and Duvall 2002; Grismer 2002; Stebbins 2003). We witnessed females mating nearly every spring, thus it is likely long-term sperm storage does not play a substantial role in their reproduction. We also observed several females copulate with males with whom they had recently over-wintered (including one translocated male). Two Resident snakes (one male, one female) over-wintered together twice (used a different den each year) and were observed copulating with each other both years following emergence. Thus, communal denning may increase the reproductive success of male *C. ruber*. Other than brief observations of newly born neonates with their telemetered mother in the maternal den, we did not find any young (< 2 years old) *C. ruber* during our study. In contrast, two of the four *C.* (*viridis*) *helleri* we encountered during our study still had their natal buttons. At least two recent encouraging studies have attempted to radio-track neonates to determine survivorship and dispersal (Cobb et al. 2005; Figueroa et al. 2005). Many more of such studies are needed to inform biologists and conservationists of this critical life-stage.

Survival – Adult mortality of *C. ruber* at the Park is apparently quite low. Very few reports on annual mortality exist for adult rattlesnakes. Reinert and Rupert (1999) report only 2 mortalities among 18 (11.1%) transmittered adult *C. horridus* over tracking periods of 101 to 351 days. Adult mortality averaged ~20% for a population of *C. atrox* (Fitch and Pisani 1993), and Nowak et al. (2002) documented mortality in only one of seven (14%) non-translocated *C. atrox*. Similarly, only 1 of 11 Resident snakes (9%) is believed to have been killed during our study. This snake was found decapitated adjacent to an animal enclosure where non-Park employees had been recently working. There were no other marks on the snake, and it is possible its death was human-caused. Dugan et al. (this volume) reported no mortalities for seven *C. ruber* over three years, a sharp contrast to the nearly 60% mortality rate of sympatric *C. helleri*. The use of cactus for refuge and limited movement distances of *C. ruber* likely adds to its high adult survivorship.

Effects of Translocation

The results of our study of translocated *C. ruber* are perhaps best described as mixed. Undoubtedly, reptiles have been translocated throughout past history by humans either intentionally or not (e.g., Brown Tree Snake, *Boiga irregularis*). A few early telemetry studies included accounts of rattlesnake behavior after relocation for *C. horridus* (Fitch and Shirer 1971; Galligan and Dunson 1979) and *C. atrox* (Landreth 1973). However, detailed studies of such activities have largely been published in the past decade. Recent relocation studies appear to fall largely into two categories, those done in an attempt to repatriate a species to a given area or to determine if relocation is a viable conservation method (Macmillan 1995; Platenberg and Griffiths 1999; Reinert and Rupert 1999; Plummer and Mills 2000; Dickinson et al. 2001; Knapp 2001; Towns and Ferreira 2001; Nelson et al. 2002; King et al. 2004), and those involving the release of animals away from areas where they were considered to be a nuisance (Sealy 1997; Hardy et al. 2001; Nowak et al. 2002; Sealy 2002; Sullivan et al. 2004; Butler et al. 2005a, b). Many of these studies have involved LDT, although a few also compared SDT, and nearly all have focused on movement behavior (including the ability to return to the original capture location) and survivorship.

Movement – Almost all of the movement parameters we calculated for the Relocated snakes were larger than Resident snakes' values for the corresponding time period. However, similar to Nowak's (1998) work with *C. atrox*, individual responses to translocation were quite varied. No overall pattern emerged between LDT and SDT in our study. Three of the translocated snakes (two SDT and one LDT) had movement parameters which were within the range of all Resident data (Fig. 2). Surprisingly, it was a SDT snake (R26) that exhibited the largest movements during the first season post-translocation (Year 1), and a LDT (R33) displayed most of the smallest movements. Although we categorized R26 as a SDT based upon how far he was relocated, it is possible he was removed from his original activity range (thus actually a LDT). However, based upon his rapid movement back toward his capture location and to an established den in early November, we believe he was familiar with the area and is properly considered a SDT.

The most commonly reported behavioral response to translocation among viperids is "aberrant" movement behavior. All three early *Crotalus* translocation studies noted marked increases in movement distances post-translocation (Fitch and Shirer 1971; Landreth 1973; Galligan and Dunson 1979); such increases have also been documented in detail for *C. horridus* (Sealy 1997; Reinert and Rupert 1999) and *C. atrox* (Nowak et al. 2002). This pattern of increased movement is apparently not unique to translocated viperids, as similar responses have been documented in colubrids (*Heterodon platirhinos*, Plummer and Mills 2000), elapids (*Notechis scutatus*, Butler et al. 2005a,b), and even a helodermatid lizard (*Heloderma suspectum*, Sullivan et al. 2004), and in non-reptiles as well.

Despite the relatively larger movement distances and ARS in Relocates (often 2-3 times greater), the magnitude of the difference between Relocates and Resident males was smaller than differences between male and female Residents. Furthermore, the Relocated movement values were all less than the mean values reported by Greenburg (2002) for resident desert *C. ruber*. Large variation in habitat use within a species between populations is not uncommon; for example, ARS for three *C. atrox* populations has been estimated as 5.4 ha (Beck 1995), 17.8 ha, and 24.3 ha (Nowak et al. 2002). These differences may stem from a variety of sources including seasonal, habitat, and calculation differences. The longer movements of Relocates, combined with their differential habitat use, suggests they may have been attempting to orient or explore their new areas (Plummer and Mills 2000). Interestingly, the fractal D analyses indicated Relocates tended to have more tortuous paths (perhaps indicative of more intensive coverage of an area) than Residents, rather than longer, linear movements that would be indicative of homing. Relocate movement values approached those of Residents in Year 2 for approximately half of the snakes (two SDT, one LDT), but increased greatly for the remainder of the LDT snakes, possibly indicating continued wandering in an attempt to investigate their new surroundings. The lone SDT with the largest Year 1 values (R26), did have reduced movement in Year 2; however, these values (ARS, total and mean distances moved) were still quite large compared to Resident males or females.

A common measure of "success" of a translocation program for nuisance snakes is rate of return to original capture locations or recurrence as nuisances (Hardy et al. 2001; Nowak et al. 2002; Sealy 2002; Sullivan et al. 2004). None of the LDT snakes returned to their capture locations, and only one of these snakes made any movements that appeared to be substantially towards its capture site. In contrast, all three of the SDT snakes returned to within 50 m of capture sites. Two of these snakes (R26, R34) returned within one month post-translocation, while the third returned in Year 2 (R27). The immediate return of two of these snakes to their capture locations may have been an attempt to orient.

Survivorship –We could detect no statistical difference in survivorship between Residents and Relocates. A cursory review of the fate of our study snakes would suggest higher mortality occurred among Relocates given only 2 of 11 (18%) Residents died compared with 3 of 6 (50%) Relocates. However, two of these deaths resulted from surgery complications, a risk inherent in any radio-telemetry study. Both a Relocate (R26, possibly stressed from relocation, albeit SDT) and a Resident (R17, not stressed from relocation) died, leaving corrected loss rates of 9% for Residents (1/11) and 33% (2/6) for Relocates. Although these surgery-related deaths occurred during transmitter renewal, another snake also similarly died (not included in this study because no field data were collected) after the implantation of its first transmitter and before it could be released. We believe the death (snake found dead in field one month after surgery) of SDT Relocate 27 was also surgery-related, which would result in an adjusted loss value of 16% (1/6) for Relocates. In contrast, the death of LDT R25 was likely a result of her translocation. She exhibited perhaps the most aberrant behavior (did not brumate, had ARS and total distance moved higher than any other female) of any of the translocated snakes, and she continually lost weight during the 16 months we followed her, despite observations of feeding.

The difference in mortality between Residents (9%) and Relocates (16%) is much smaller than has been seen in most other snake translocation studies. Plummer and Mills (2000) found resident Hognose snakes (*Heterodon platirhinos*), survived three times longer than translocates even though annual adult mortality for resident Hognose snakes was already 50%. Similarly, translocated *C. horridus* in Pennsylvania suffered 55% mortality compared to 11% for resident snakes (Reinert and Rupert 1999). In two studies of translocation effects on *C. atrox*, mortality rates of moved individuals were 57% and 71% (Nowak et al. 2002). All three of these high-mortality studies involved long-distance translocations. In contrast, Sealy (1997) did not record any deaths among five SDT *C. horridus* followed from one to three seasons. Had there not been surgery complications, we believe all of our SDT snakes would have experienced the same survivorship as Resident snakes.

It is tempting to suggest that the apparently high intrinsic annual survivorship for non-translocated *C. ruber* may have insulated the mortality rates for the translocated snakes. Deaths in translocated snakes have been attributed to several factors including over-winter mortality in snakes not finding appropriate den sites (Reinert and Rupert 1999), increased exposure to humans (Nowak et al. 2002), and a general consensus that their aberrant movements may increase exposure to predators

(Plummer and Mills 2000). The successful location of an established den by LDT R28 in Year 1 and by LDT R33 in Year 2 is encouraging for conservation purposes. Because of the relatively mild climate throughout most of the range of *C. ruber*, these snakes can and do survive winter in a variety of locations, including under *Opuntia* (see Dugan et al. this volume). Thus, the failure to locate a suitable den the first winter is not necessarily fatal for translocated *C. ruber* (although it may have contributed to the death of R25).

We suspect R28 used conspecific trailing of Residents to locate the established den in 2001, and it appears R33 (released a year after R28) may have trailed R28 in 2002 to locate the same den. The repeated close location (5 to 30 m) of R33 to locations recently used by R28 is similar to the associations seen between translocated *C. horridus* by Reinert and Rupert (1999). It is possible that repatriations of snakes into areas with low den availability and long devoid of residents may make finding suitable dens difficult for many species.

Final Considerations

The debate over the efficacy of translocation as a conservation management tool for reptiles and other organisms has been well discussed (Griffith et al. 1989; Burke 1991; Dodd and Seigel 1991; Dodd 1993; Sealy 1997; Whiting 1997; Hardy et al. 2001; Shine and Koenig 2001). Clearly translocation of individuals can have dire consequences and should not be undertaken lightly. The contrast between LDT and SDT approaches in nuisance snake management has stemmed from an effort to balance the often divergent needs of minimizing long-term harm to the snake while attempting to assuage the concerns of stakeholders.

The use of SDT as a management tool may work for certain human user groups and certain snake species (Nowak et al. 2002; Sealy 2002), but not others (Sullivan et al. 2004). In fact, Hardy et al. (2001) ceased recommending SDT as a management technique for *C. m. molossus* and *C. atrox*, after observing high return rates among SDT individuals. The use of SDT to manage nuisance *C. ruber* may be feasible under certain circumstances, although all three SDT snakes returned to the vicinity of their capture at some point. Had the capture locations been in housing tracts instead of animal pens staffed by creature-friendly Park employees, the return of the snakes may have been quite unwelcome. It was promising to see that two of the SDT snakes quickly left the capture area and stayed well clear of it for the remainder of the study. The SDT of the three *C. ruber* in this study did not appear to be detrimental to the snakes, and SDT may still be preferable to the destruction of this sensitive species when human-snake conflicts must be mediated.

There are, in fact, two ways to interpret the results of our LDT efforts. A strong argument could be made that LDT obviously resulted in aberrant movement behavior (stress) and likely resulted in the death of one of our three LDT snakes. Nearly all previous studies involving LDT efforts have ultimately recommended against such activities by humans (Reinert and Rupert 1999; Plummer and Mills 2000; Hardy et al. 2001; Nowak et al. 2002; Sealy 2002). The hazards of LDT are many, especially if the receiving area already supports a population, including increased mortality, potential disease transmission, increasing population numbers above carrying capacity, and outbreeding depression (Griffith et al. 1989; Burke 1991; Dodd and Seigel 1991; Dodd 1993; Sealy 1997; Whiting 1997; Hardy et al. 2001; Shine and Koenig 2001). Based upon these previous studies and our results, we cannot recommend the use of LDT as an effective management tool for nuisance *C. ruber*.

Alternatively, we could argue that two out of three of our LDT snakes were able to successfully locate dens, forage, were observed mating, and appear to have established stable activity ranges. Given the pace of development in southern California, there will likely come a time when fragments of preserved or restored habitat may need repatriation of *C. ruber*. Thus, while not effective for mitigating human-snake conflicts, LDT activities may still have a role in rattlesnake conservation. As mentioned in Moorbeck (1998), high mortality rates are often seen in the early stages of many captive breeding, head-starting and reintroduction programs. Yet with experience and further research, survivorship can be increased. Successes will likely be species, and perhaps individual, dependent. The relatively constrained movements of *C. ruber* may be beneficial in the conservation of this species on small fragments. Plummer and Mills (2000) suggested sedentary snake species might be less affected by translocation than those with normally wide-ranging behavior. Both timing of release and the quality of the receiving habitat are important considerations. If the receiving habitat includes large rock outcrops suitable for denning and possesses or can be augmented with

Opuntia , establishment of new *C. ruber* populations may be possible. Ultimately, a careful consideration of several factors will be necessary for each species and situation, and alternative conservation strategies examined.

Regardless of the method used for managing nuisance rattlesnakes, perhaps the greatest contribution academics, agencies and naturalists can make towards rattlesnake conservation is the education of the public. Perhaps the easiest way to minimize any negative effects of translocation on rattlesnakes is to nullify the original need for their relocation. A detailed discussion on the creation and prevention of nuisance rattlesnakes is presented in Nowak et al. (2002), and we similarly stress the need for outreach efforts. Education of the public about common rattlesnake misperceptions, ways to minimize attracting rattlesnakes, and the potential harm to the snake if removal is insisted upon (especially over long distances) can be effective. For example, in their study on Gila Monster translocations, Sullivan et al. (2004) received encouraging support from affected homeowners and suggested public education can reduce the need for translocations of this venomous lizard. Several programs exist to educate the public about living with various wildlife species (e.g. Keep Me Wild, California Department of Fish and Game; mountain lion presentations, Wildlife Health Center, UC Davis Veterinary School). Similar active outreach programs and presentations should be further developed for rattlesnakes to augment already existing paper and web-based education materials. Through such efforts, the demand for rattlesnake relocations can hopefully be greatly reduced.

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Table 1 – Study dates, duration and fate of radio-tracked Northern Red Diamond Rattlesnakes (*Crotalus ruber)*. Status indicates if a snake was considered a Resident (not relocated) or Relocated (moved to new location after transmitter implantation).

I.D.	Sex	Status	Capture Date	Final Date	Days Tracked	Fate
C13	♂	Resident	Aug-99	Jun-03	1373	Trans. failed early; found alive 11/05
C14	♀	Resident	Aug-99	Jun-03	1363	Trans. failed early
C15	♀	Resident	Sep-99	Jan-02	836	Found depredated
C16	♂	Resident	Sep-99	Aug-03	1394	Trans. failed early
C17	♂	Resident	Oct-99	Nov-00	395	Died-surgery complications
C18	♀	Resident	Oct-99	Oct-01	711	Unknown
C19	♂	Resident	Oct-99	Oct-03	1439	Trans. removed, snake released
C20	♀	Resident	Oct-99	Dec-02	1152	Trans. failed early
C24	♂	Resident	Oct-00	Jul-04	1361	Trans. removed, snake released
C29	♀	Resident	Feb-02	Feb-04	717	Trans. removed, snake released
C30	♀	Resident	Feb-02	Feb-03	349	Not recaptured
R25	♀	Relocate	Jun-01	Nov-02	515	Died-disease
R26	♂	Relocate	Jul-01	Feb-03	569	Died-surgery complications
R27	♂	Relocate	Jul-01	Apr-03	622	Died-surgery complications
R28	♂	Relocate	Aug-01	Feb-04	900	Trans. removed, snake released
R33	♂	Relocate	Jul-02	Jul-04	746	Trans. removed, snake released
R34	♀	Relocate	Jul-02	Nov-03	506	Not recaptured

Table 2 – Summary of activity range size (ARS), movement distances (Dist.) and speed (total distance/total days) for Resident *C. ruber*. Actual locations indicate the number of times a snake was tracked, unique locations indicate the number of locations used to calculate movement data.

I.D.	Sex	Actual (unique) Locations	Mean ARS (ha)	Mean Dist. per year (km)	Mean Dist. per move (m)	Mean Speed (m/day)
C14	♀	108 (82)	0.65	0.77	35.3	3.4
C15	♀	55 (33)	0.62	0.41	27.4	2.4
C18	♀	56 (42)	0.59	0.63	32	3.5
C20	♀	92 (75)	1.24	1.1	49.7	4.4
C29	♀	45 (39)	0.72	0.74	40.7	3.9
C30	♀	31 (24)	1.47	0.96	41.9	3.8
C13	♂	58 (50)	1.10	0.83	46	4.1
C16	♂	97 (72)	1.93	1.14	67	5.3
C17	♂	18 (18)	2.51	1.58	93	10.1
C19	♂	114 (79)	4.43	1.67	88.4	7.8
C24	♂	98 (62)	4.02	1.68	83	6.9
Female Grand Mean			**0.88**	**0.77**	**37.8**	**3.6**
Male Grand Mean			**2.80**	**1.38**	**75.5**	**6.8**
t statistic			-3.81	-2.98	-4.50	-3.68
P value (one-tailed)			0.002	0.008	0.001	0.003

Table 3 – Summary of movement behavior of translocated *C. ruber*. Year 1 (Y1) data are from the first move after translocation until December of that year; Year 2 (Y2) data are from the second activity season post-translocation (Jan.-Dec.). All distances (Dist.) are in meters, and activity range size (ARS) are in hectares (ha).

Snake ID	Sex	Dist. Relocated	No. of Locations		ARS (ha)		Dist. per Year		Mean Dist. per Move		Mean Daily Speed	
			Y1	Y2	Y1	Y2	Y1	Y2	Y1	Y 2	Y1	Y2
Short Distance Translocates												
R34	♀	97	16	23	1.66	1.39	756	1004	50	46	4.6	3.5
R27	♂	149	17	28	6.54	4.45	1461	2164	91	80	12.6	6.8
R26	♂	340	18	23	14.96	6.22	2230	2329	131	106	18.1	8.3
Long Distance Translocates												
R33	♂	856	18	27	1.87	9.52	543	2795	32	108	3.1	9.0
R28	♂	893	11	17	2.77	3.72	984	1556	98	97	11.2	4.5
R25	♀	1090	19	19	7.34	14.13	1659	2209	92	123	11.1	7.4

Figure 1 – Study site overview and representative annual activity range polygons for Resident (open) and Relocated (hatched) *C. ruber*. Thick outlines indicate female polygons, thin outlines indicate male polygons. Resident polygons include all points from a single representative year and Relocate polygons are from the year the snakes were initially moved (Year 1). For comparison, Resident activity ranges from the comparable time period (Jun. to Dec.) to the shown Relocate Year 1 data were typically 40% smaller (range 6 to 67%; not shown).

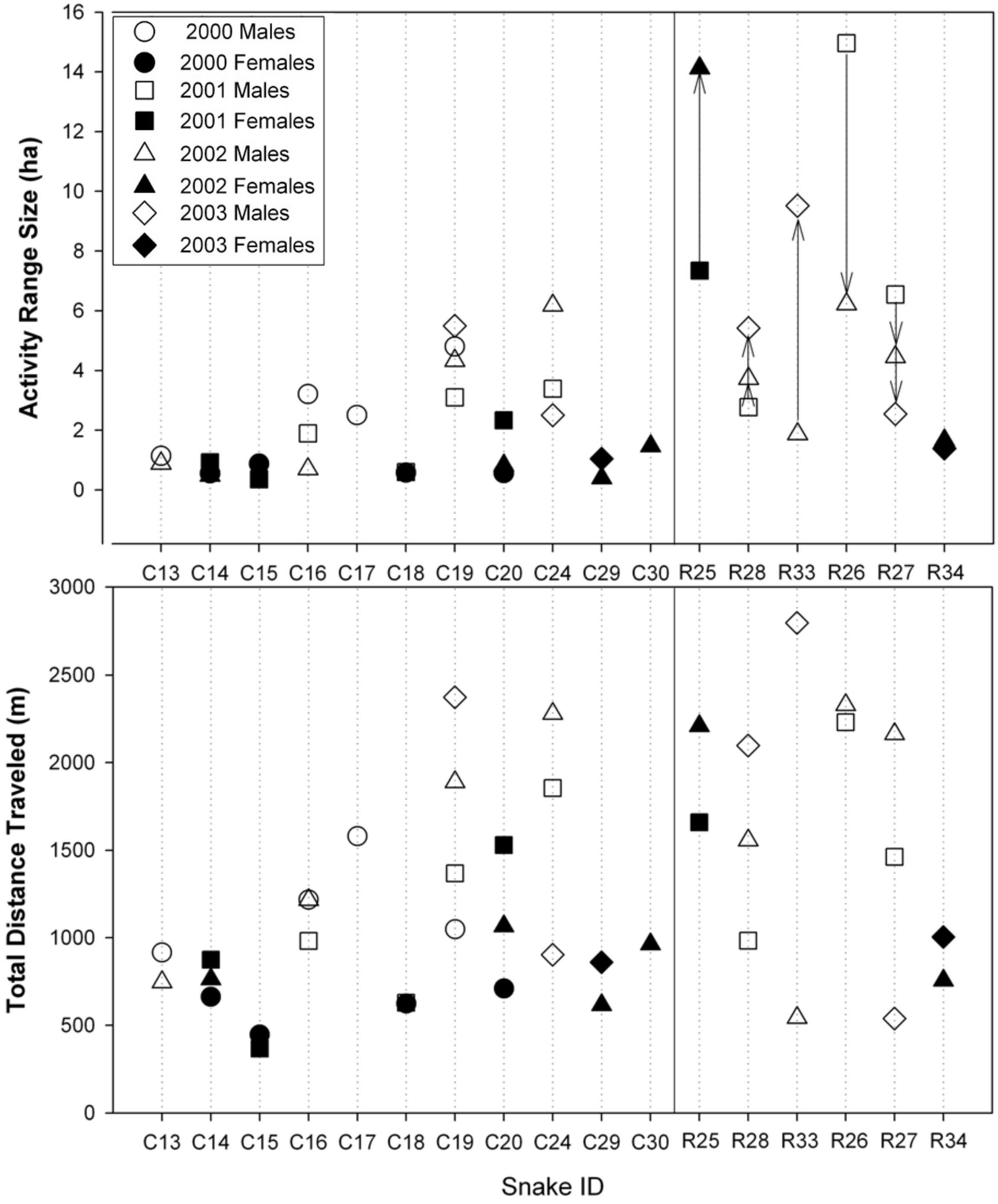


Figure 2 – Annual activity range sizes and total distances moved per year for Resident (C13-C30, left panels) and Relocated (R-25-R33, right panels) *C. ruber*. The Relocated snakes are arranged (left to right) according to the relative distances they were move (greatest to least). Arrows in top right panel indicate change in ARS size for Relocates from Year 1 to Year 2 to Year 3.

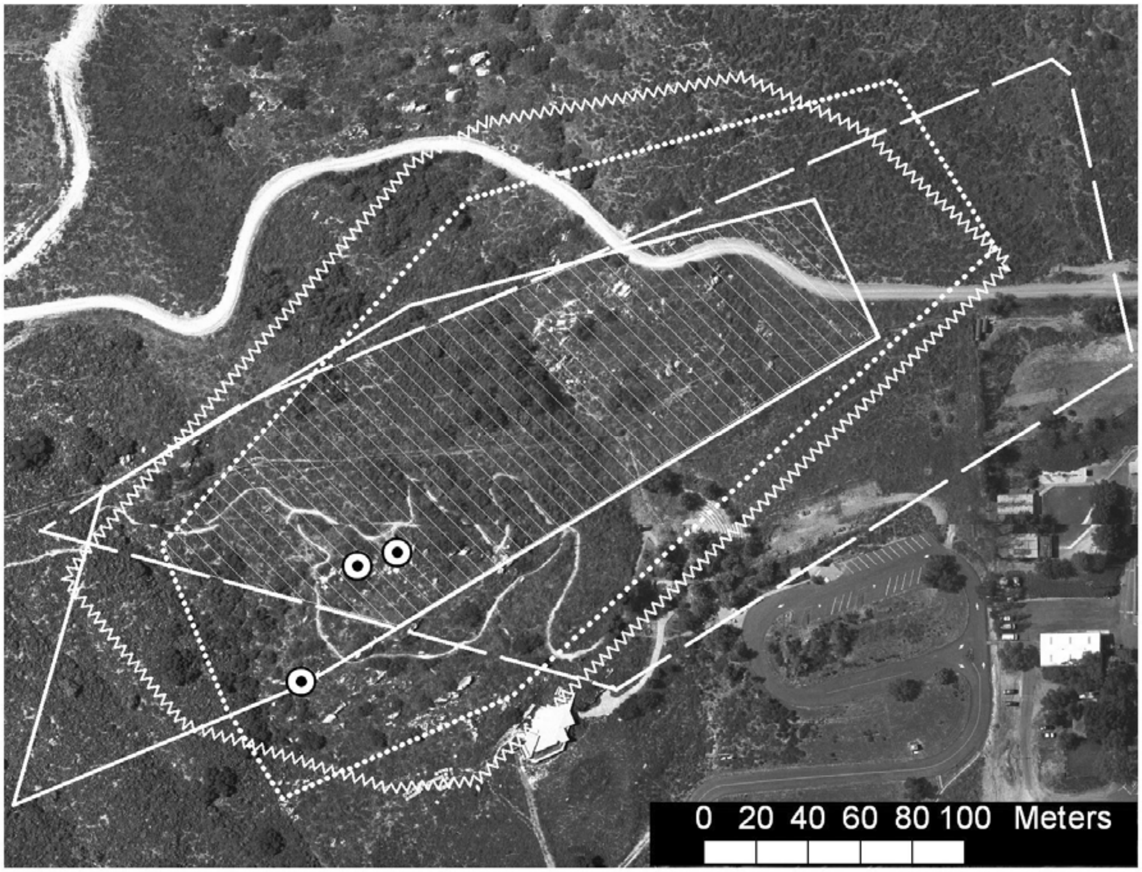


Figure 3 – Estimated annual activity range polygons for Resident Male C19. Each polygon encloses all location points during 2000 (dashed line), 2001 (solid line), 2002 (dotted line) and 2003 (zig-zag line). Diagonal hatching indicates enclosed area used every year by C19 (core habitat). Circle-dot symbols indicate location of winter dens.

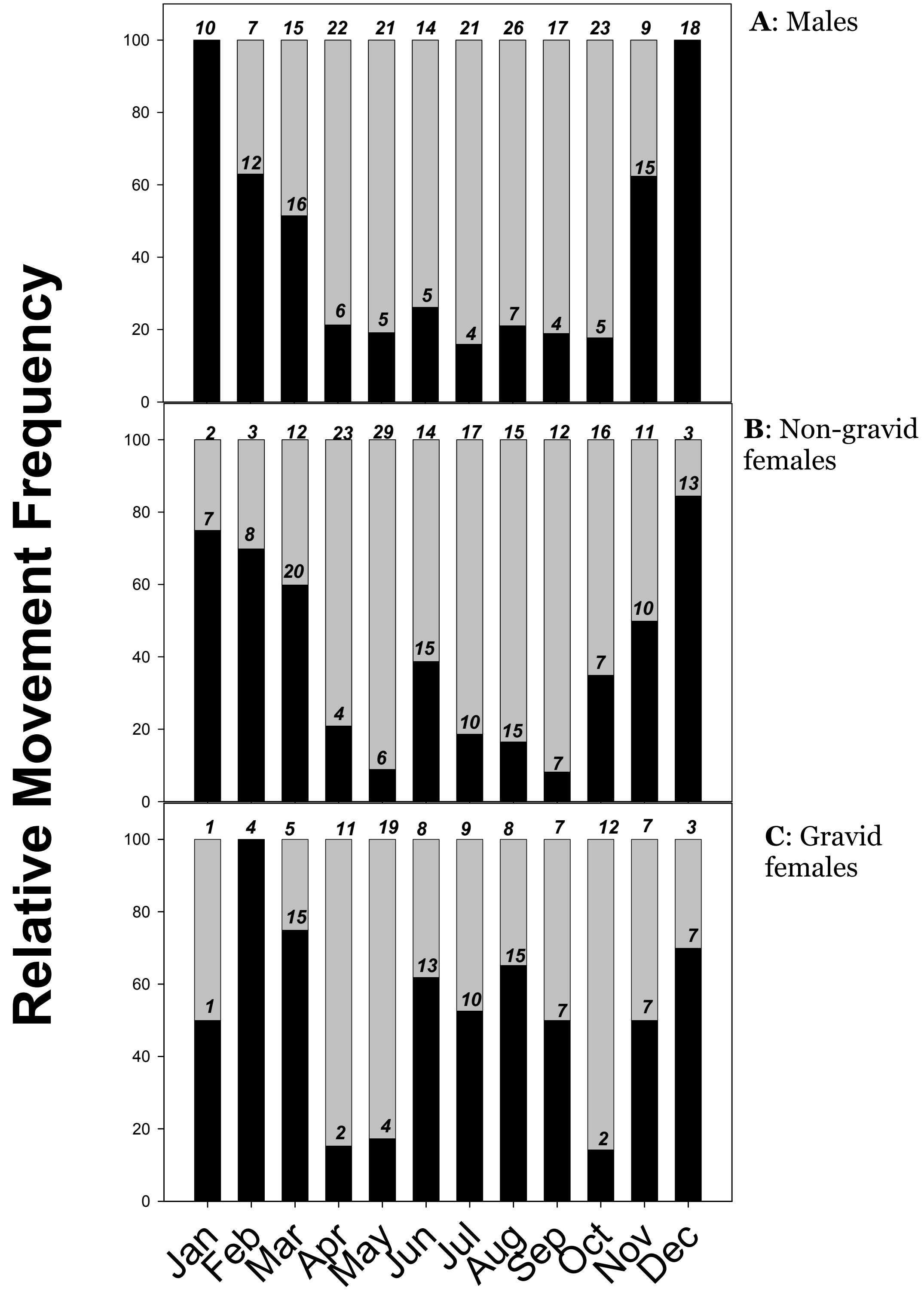
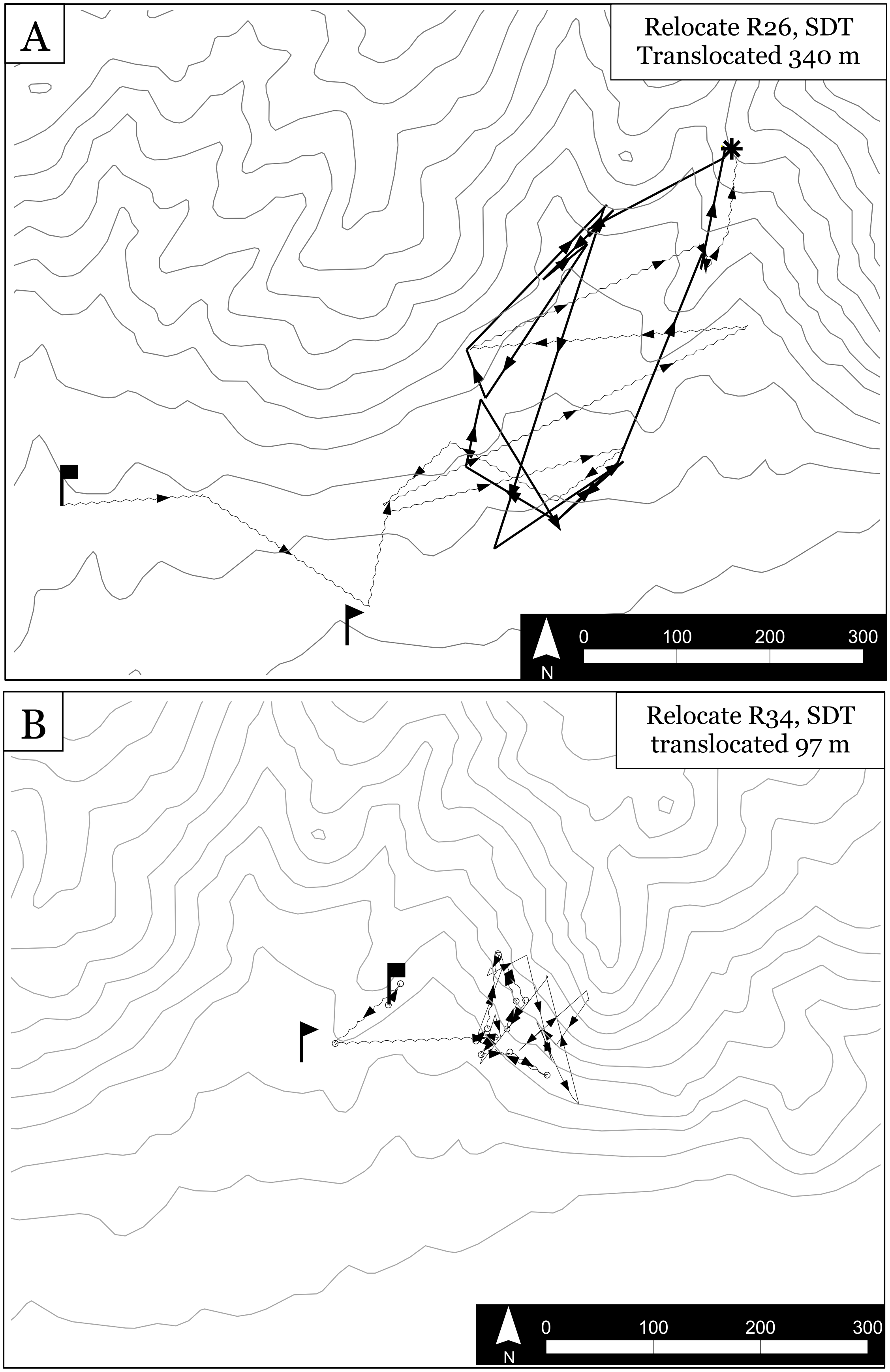
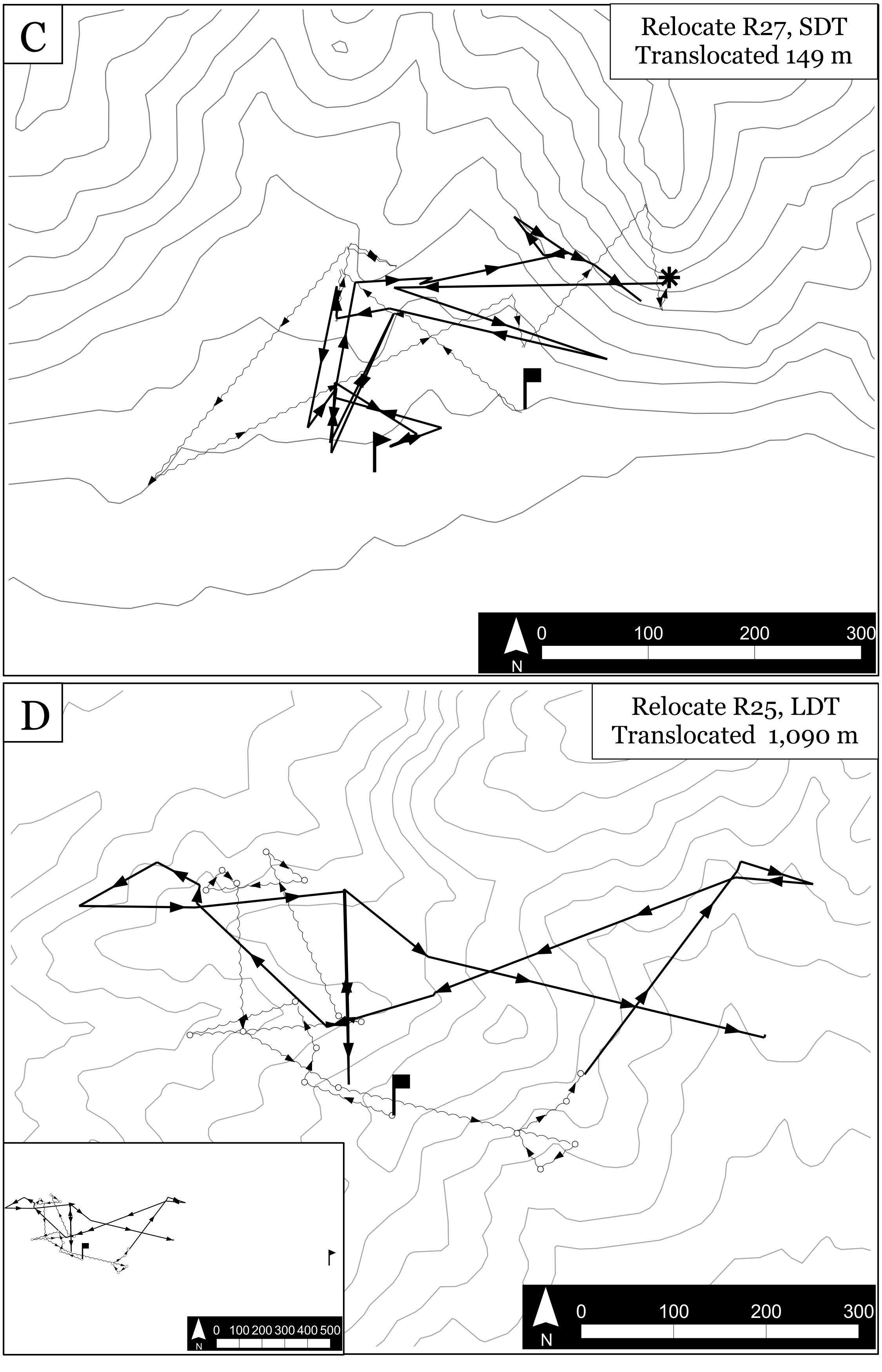
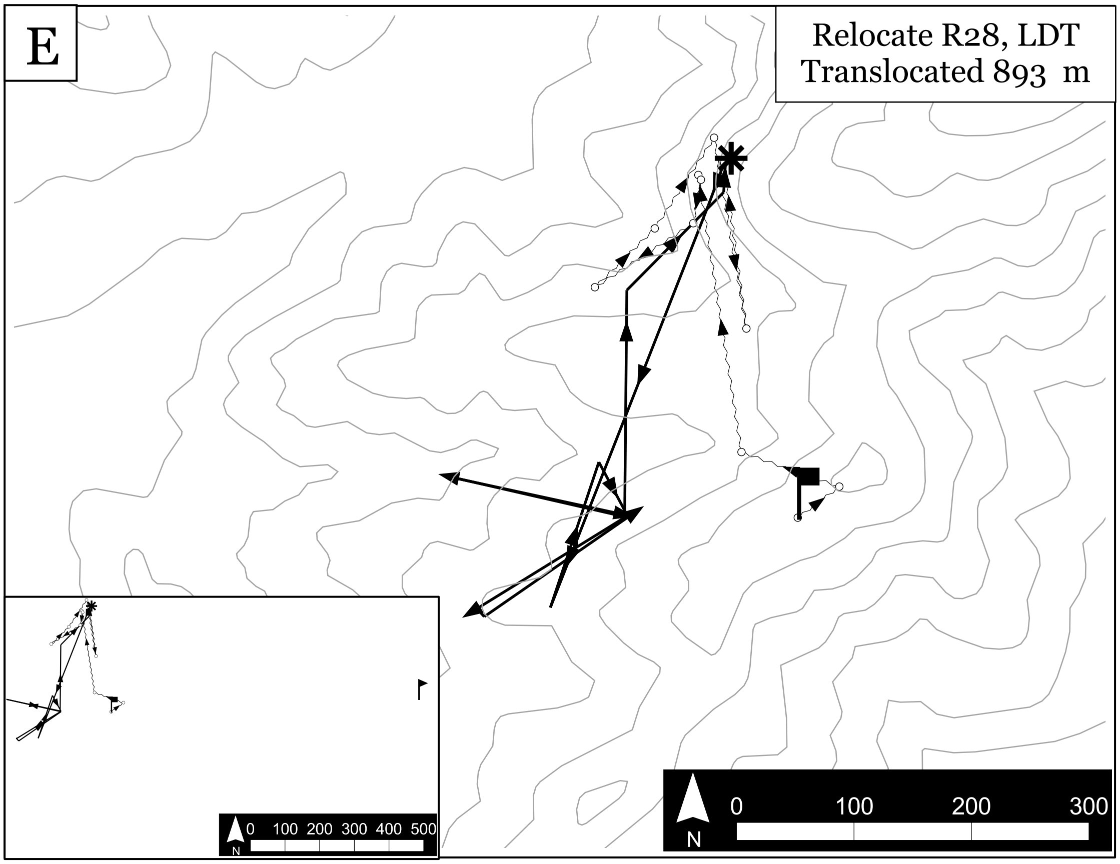


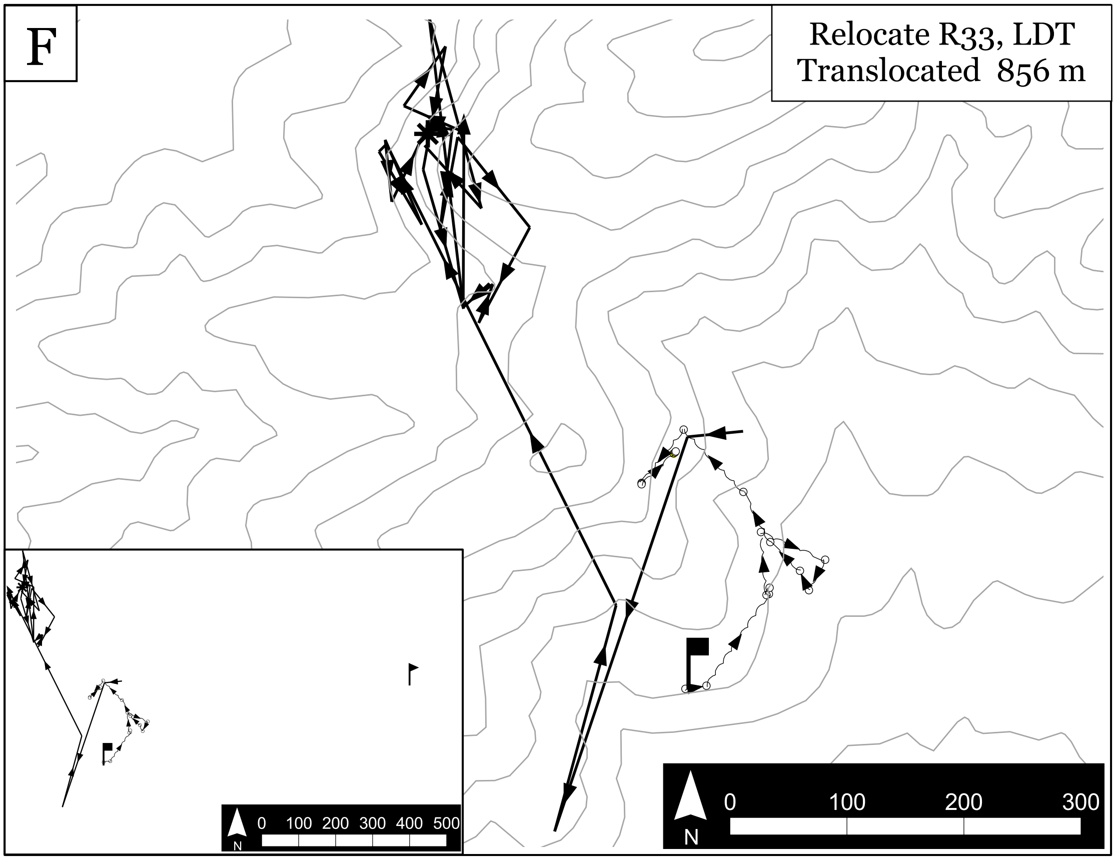
Figure 4 – Relative movement frequencies for Resident *C. ruber*. Dark portion of bars indicates no movement, grey portion indicates snake moved more than 5 meters, numbers are sample sizes.

Figure 5 – Annual movement distances and directions of translocated *C. ruber*. Panels A-C represent short-distance translocates (SDT), panels D-F represent long-distance translocates (LDT). Flags indicate capture (triangle flags) and release (square flags) locations; lines indicate Year 1 (scalloped) and Year 2 (solid) movements. Panel D-F insets (500 m scale) indicate relative distance and direction LDTs were relocated compared to subsequent movements shown in primary panel (300 m scale). Star graphics indicate brumation sites, and all distances are in meters.


A
Relocate R26, SDT
Translocated 340 m
0
100
200
300
N
B
Relocate R34, SDT
translocated 97 m
0
100
200
300
N


C
Relocate R27, SDT
Translocated 149 m
0
100
200
300
N
D
Relocate R25, LDT
Translocated 1,090 m
0
100
200
300
N
0
100
200
300
400
500
N


E
Relocate R28, LDT
Translocated 893 m
N
0
100
200
300
N
0
100
200
300
400
500


F
Relocate R33, LDT
Translocated 856 m
N
0
100
200
300
N
0
100
200
300
400
500