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Human–Wildlife Conflict at a Suburban–Wildlands Interface: Effects of Short- and Long-Distance Translocations on Red Diamond Rattlesnake (*Crotalus ruber*) Activity and Survival

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Abstract: The mitigation of human–rattlesnake conflicts often involves euthanizing or translocating the offending rattlesnake. Although translocation is generally considered more humane, especially by the general public, it may negatively impact the translocated individual and may not be effective if that individual returns to areas where the probability of human conflict is high. We used radiotelemetry to experimentally study the effects of short- (SDT) and long-distance translocation (LDT; beyond the typical home range or activity range) on adult Red Diamond Rattlesnakes (*Crotalus ruber*) near a residential development in Southern California. Though the results were mixed, some analyses suggested that higher numbers of SDTs were associated with larger activity areas and increased movement. For snakes undergoing LDT, the activity areas and mean daily movement distances were 1.8–4.6 times larger than those of non-LDT snakes in the year of translocation, but were similar in the following year. Cox regression models revealed that, for both LDT and non-LDT snakes, every 1 m increase in the distance moved resulted in a 1.2% decreased risk of moving back into a human-modified area and a 1.6% decreased risk of returning to the original site of conflict. We failed to detect an effect of either LDT or SDT on body mass change or survival. Our findings suggest that LDT of nuisance snakes may be a viable option for at least some rattlesnake populations or species, especially those in which individuals do not require communal overwintering sites.

Keywords: reptiles; Serpentes; snakes; Viperidae; Crotalinae; human–wildlife coexistence; urban ecology; mortality

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1. Introduction

As human development encroaches on natural areas, human interactions and conflicts with native wildlife increase [1–5]. In many cases, conflict can provide a basis for public interest in native species and their conservation, and promote coexistence. However, these interactions too often become undesirable, with wildlife either causing property damage or injury to humans, or being perceived as causing such. Three options exist to mitigate human–wildlife conflicts: (1) limit human access to conflict areas; (2) remove the offending animals; or (3) learn to tolerate the conflict. Limiting human access to potential conflict areas has proven effective at minimizing disturbance to wildlife and risks to humans [6–8]. Limiting access, however, is predicated on identifying conflict areas and having the legal authority to limit access. The latter becomes particularly acute when nuisance wildlife moves onto private property, as a person’s access to their property cannot be limited. In such cases, removing the offending animal is the only option, apart from doing nothing, though education can enhance tolerance.

Animals removed from conflict with humans are dealt with either by euthanization or translocation [5,9]. Translocation refers to physically moving one or more individuals

and broadly covers many practices, such as establishing, reestablishing, or augmenting populations [10–12]. Mitigation translocation, the practice of moving nuisance wildlife to areas where conflict with humans no longer exists [13–15], is preferred and more humane than euthanization [14]. However, many studies examining the effects of translocation urge caution because of increased mortality, ineffectiveness, and/or negative effects on other wildlife. Translocated animals often exhibit erratic movements and suffer high mortality rates, at least in the short-term [5,13,16–27], and may also experience elevated stress [28]. Additionally, translocated animals could return to the original area or move into a new conflict area [13,16,29–33]. Finally, translocated animals may negatively affect resident wildlife by introducing disease, disrupting their social structure, or contributing to outbreeding depression [11,13,16,34–36]. Typically, animals subjected to short-distance translocation (SDT) suffer fewer consequences, but are more likely to return to conflict areas compared to animals subjected to long-distance translocation (LDT [16]).

In the United States, venomous snakes often come into conflict with humans [37,38]. Even though public perception of the risk may be inflated [31,39], they do represent a legitimate risk. Mortality from venomous snakebites in the U.S. is low (five to seven deaths annually), but it remains a significant medical issue, with an estimated 2683–3858 envenomations annually [40]. These envenomations incur substantial costs and physical and emotional distress [41–43]. Unfortunately for venomous snakes, there is some public support for euthanizing nuisance animals [44]. Because venomous snakes are chiefly top-order predators, indiscriminate euthanization is problematic as the loss of individuals could have ecological ramifications [13,45,46]. Euthanization may also be problematic when the nuisance species is endangered or protected, thereby countering conservation efforts and contradicting legal mandates [37]. Because SDT can alleviate the negative effects of translocation [16], it may effectively manage nuisance rattlesnakes [47], especially when the measures are to reduce the chance of return to conflict areas [48]. Despite one author reporting success with SDT [37], others have reported snakes returning to conflict areas [31,49,50].

Despite a number of studies examining translocation in rattlesnakes, many have methodological weaknesses. Several studies used radiotelemetry to monitor venomous snakes translocated for establishing or reestablishing populations [51–58]. While such studies provide valuable information on the behavior of translocated snakes, they lack non-translocated (NT) control snakes. Other studies have used mark/recapture methods [31], but such methods are poorly suited for determining snake mortality and how often snakes return undetected to conflict areas. A few studies have used radiotelemetry and appropriate control groups. Most of these studies revealed increased movements and size of activity areas in LDT relative to SDT snakes [28,49,50,59–62]. Some studies further concluded that LDT snakes suffered higher mortality [48,59], whereas others did not [49]. To date, no studies have directly compared SDT, LDT, and NT snakes. Although Brown et al. [49] attempted to compare all three groups, the unfortunate deaths of two of three SDT snakes due to surgical complications precluded statistical analyses.

In this study, we used radiotelemetry to experimentally examine the effects of SDT and LDT on the survival and spatial ecology of adult Red Diamond Rattlesnakes (*Crotalus ruber*) to inform future policies for dealing with nuisance rattlesnakes. Because the species is protected in southern California due to anthropogenic threats [63], euthanization is undesirable as an option for mitigating human–wildlife conflicts. Although several criteria have been used to distinguish SDT and LDT in rattlesnakes (e.g., [31,47–49]), we considered SDT to be within and LDT to be beyond the typical home range or activity range of individuals in the study population.

2. Materials and Methods

2.1. Study Site

We conducted the study in the southern portion of Loma Linda, California (34°02' N, 117°16' W), within a ca. 500 ha boundary area between a suburban residential area to the north and a largely undeveloped area of rolling hills (ca. 324 km²) extending southeast (Figure 1). The portion containing natural habitat consisted largely of non-native grassland, with steeper north-facing slopes classified as coastal sage scrub dominated by California Sagebrush (*Artemisia californica*) and Black Sage (*Salvia mellifera*), and south-facing slopes populated by Brittlebush (*Encelia farinosa*). The site lacked the rock outcrops and substantial cactus patches preferred by *C. ruber* elsewhere [64,65]. Human development was largely residential, with sprinkler-irrigated lawns and gardens, and non-native tree species. The study area also contained small citrus orchards on the eastern end and a large cemetery on the western end, which included large trees and year-round sprinkler-irrigated lawns. The site experiences a Mediterranean climate [66], with much of the 34.4 cm average annual precipitation occurring during the winter and spring [67]. Winters are mild, with the mean daily low temperature in January being 4.1 °C. Summers are hot and dry, with the mean daily high temperature in July being 34.7 °C [67].

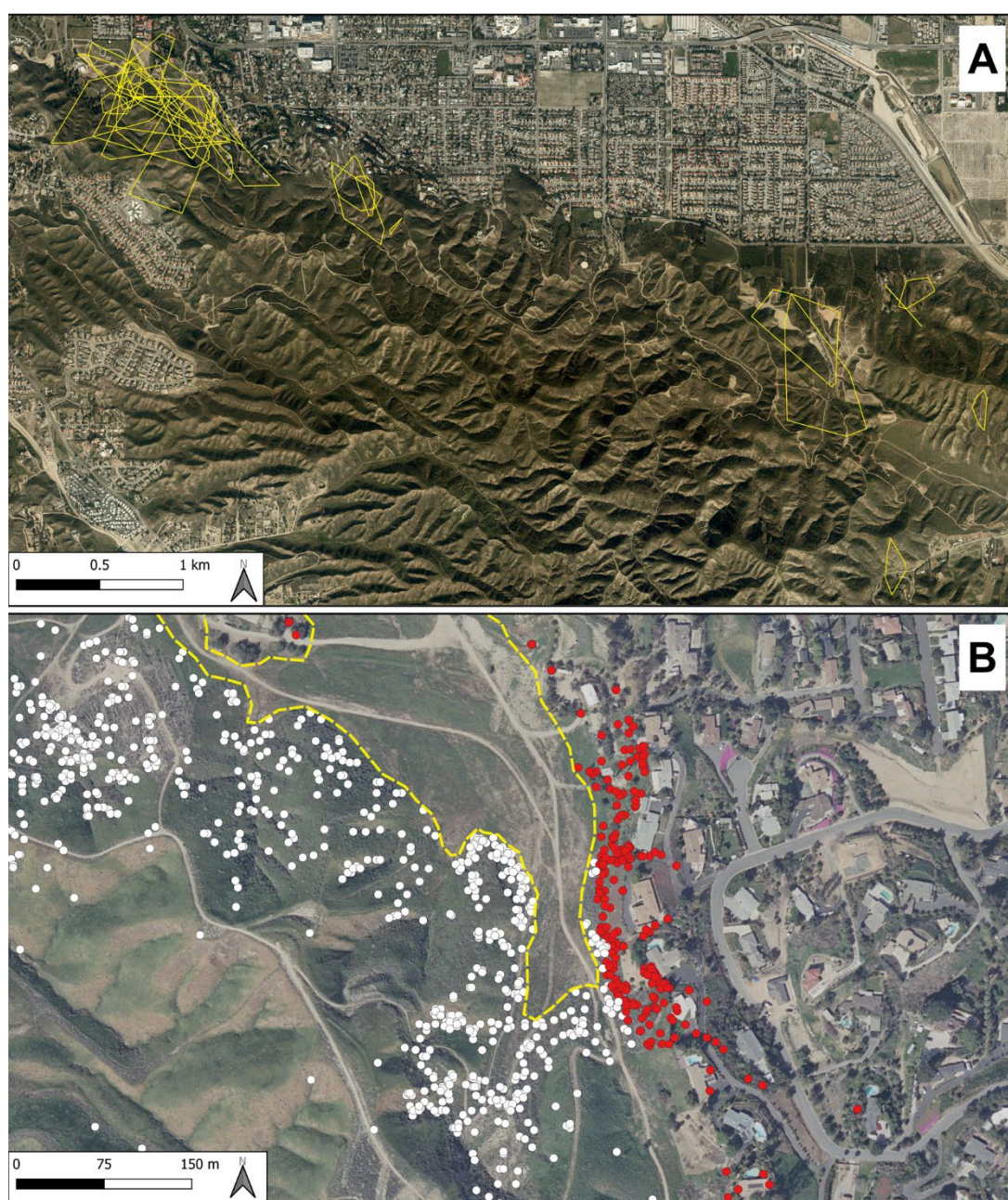


Figure 1. (A) Study site in Loma Linda, California, USA, showing the 100% minimum convex polygons (MCPs) for all fixes of all radiotelemetered Red Diamond Rattlesnake (*Crotalus ruber*) in the study with three or more unique fixes ($n = 29$). (B) Spatial depiction of a western portion of the study site. Radiotelemetry fixes (all snakes pooled) are shown for natural habitat (white circles) versus human-modified areas (red circles). Yellow dashes outline a plowed firebreak that the snakes moved across, but never stopped within.

2.2. Legal Issues

The study required cooperation from residents, who reported snakes and allowed access to their property. To solicit assistance, we distributed fliers to property owners bordering the natural habitat. Because our study involved potential liability due to the possibility of envenomation from our research subjects, we sought legal advice and developed a letter informing homeowners of the nature of our research. The letter included an agreement that allowed homeowners to specify their level of permission for us to access their property and their wishes regarding the protocol to follow when we discovered snakes on their property. Of the 28 homeowners that signed the agreement, 27 granted us access

to their property and all requested that any accessible snakes be translocated away from their property. Homeowners were informed if a snake on their property was inaccessible (e.g., beneath wooden patios or concrete slabs). Thus, these legal issues necessarily constrained our study design, including our ability to assign snakes to an NT group.

2.3. Radiotelemetry

We began snake collection, radiotransmitter implantation, and tracking in July 2008 and continued through December 2011. We obtained most snakes through cooperating residents who contacted us when they discovered a rattlesnake on their property. We also collected snakes opportunistically when discovered in the field, especially during the spring mating season (February–April [64]). We determined sex by subcaudal scale count (male: ≥ 24 ; female: ≤ 23) and/or probing using Neosporin-lubricated sexing probes. We measured the total length via photography in a press box [68] with the floor covered by 1 cm graph paper. Photographs were imported into ImageJ version 1.47q [69] to calculate snake length. We measured snake mass initially, and again when we returned to the lab for transmitter replacement or injury, using a 2500 g Pesola spring scale (Pesola AG, Baar, Switzerland).

We implanted SI-2 (Holohil Systems Ltd., Ottawa, ON, Canada) and SOPB-2190 (Wildlife Materials Inc., Murphysboro, IL, USA) radiotransmitters that weighed ca. 6 and 9 g, respectively, and always represented $<5\%$ of an individual's body mass [60]. Surgical procedures followed the protocols established for snakes [70,71]. To reduce post-surgical mortality [70], we released the snakes soon (24–48 h) after surgery. We obtained fixes on each snake's location 1–2 times weekly using a Telonics TR2 receiver (Telonics, Mesa, AZ, USA) and a generic four- or six-element Yagi antenna. For each fix, we attempted to locate the snake visually and record its coordinates using a handheld GPS unit (Magellan Explorer 210; Magellan, Santa Clara, CA, USA). If a snake was not visible, we took the coordinates as close to the source of the strongest radio signal as possible.

2.4. Translocation Protocol

After transmitter implantation, we initially released snakes at either the site of capture if found in natural habitat, or 50–400 m away in the nearest natural habitat (SDT-translocated) if caught in or near human-modified areas (usually at the landowner's request). Once released, the snakes were disturbed as little as possible when tracking their movements. However, because of the risk of injury to humans (and the snake), and for the legal reasons discussed above, we SDT-translocated (50–400 m) any accessible telemetered animal found on a homeowner's property or in areas where direct conflict with humans was deemed likely. Thus, snakes could be SDT-translocated more than once, and we recorded all such translocations.

In October 2009, we began randomly assigning some newly captured snakes to the LDT group. These snakes, with three exceptions (see below), were moved ≥ 716 m away from their capture site and into natural habitat. We adopted the 716 m criterion used by Brown et al. [49], who distinguished SDT and LDT based on the maximum straight-line distance between any two locations for non-translocated *C. ruber* at a study site relatively close to ours. In retrospect, the greatest straight-line distance of any non-LDT snake at our study site was 681 m, supporting our interpretation that snakes assigned to the LDT group met the formal definition of long-distance translocation. No snakes were moved >6 km.

Deviations from the SDT/LDT schema included three snakes. One female (Snake 19, Table 1), initially translocated 519 m, displayed erratic movements subsequent to release. Given that female *C. ruber* have significantly smaller home ranges than males [49], we interpreted these erratic movements as translocation out of her normal home range, and therefore re-assigned her to the LDT group. An additional female and male (Snakes 2 and 11 respectively, Table 1) in the eastern portion of the study site, where we had access issues, were reassigned 1 year later from the non-LDT group to the LDT group after we translocated them to the western portion of the study site. These two snakes, subjected to

both the non-LDT and LDT conditions, were treated as separate snakes (Snakes 2.1 and 11.1, Table 1) in our analyses. Thus, we had minor pseudoreplication across, but not within, treatment groups; the latter would have been more problematic.

Table 1. Attributes and fates of the radio-tracked adult Red Diamond Rattlesnakes (*Crotalus ruber*) near Loma Linda, California, USA. LDT indicates whether the snake was translocated a long distance (>716 m) to a new location after transmitter implantation (yes or no). SDTs indicates the number of short-distance (<716 m) translocations. Dates indicate the range of telemetry data collection. Change in mass (Δ) represents the difference between the initial and last mass recorded if recaptured.

I.D.	Sex	LDT	SDTs (#)	First Date	Last Date	Days Tracked	Total Fixes	Δ Mass (%)	Fate
2	♀	No	3	8/2/2008	6/10/2009	313	62	−21.4	Translocated to become snake 2.1
2.1 ^a	♀	Yes	0	10/14/2009	10/21/2009	14	5		Died—killed by human action
3	♀	No	6	8/3/2008	10/12/2011	1145	180	−7.1	Transmitter removed, snake released
4	♀	No	0	8/10/2008	8/23/2009	384	68	25.0	Died—found depredated ^d
5	♂	No	1	8/27/2008	2/16/2010	539	92	−19.2	Died—second surgery complications
6	♂	No	13	8/27/2008	10/12/2011	1121	151	13.2	Transmitter removed, snake released
7	♀	No	1	9/1/2008	9/15/2009	382	63		Lost—suspected transmitter failure ^c
10	♂	No	1	9/16/2008	12/8/2008	88	3		Died—injury/surgery complications
11	♂	No	4	10/9/2008	10/14/2009	350	52	0.0	Translocated to become snake 11.1
11.1 ^a	♂	Yes	0	10/21/2009	10/18/2011	721	90	18.8	Transmitter removed, snake released
12	♀	No	2	10/9/2008	5/7/2009	212	34		Lost—suspected transmitter failure ^c
13	♂	No	1	10/21/2008	11/21/2008	36	6		Lost—suspected transmitter failure ^c
14	♂	No	1	1/11/2009	1/27/2009	26	3		Died—suspected depredation ^d
15	♀	No	1	1/26/2009	7/31/2009	193	31		Lost—suspected transmitter failure ^c
16	♀	No	1	3/13/2009	10/11/2011	929	165	−32.1	Transmitter removed, snake released
17	♀	No	3	3/19/2009	1/28/2010	215	42	−35.2	Died—illness
18	♂	No	0	3/19/2009	3/27/2009	11	2		Lost—suspected transmitter failure ^c
19 ^b	♀	Yes	8	10/14/2009	10/17/2011	706	131	27.3	Transmitter removed, snake released
20	♂	No	3	10/21/2009	7/26/2011	631	122		Died—killed by human action
21	♀	Yes	13	4/7/2010	10/11/2011	559	80		Transmitter removed, snake released
22	♂	Yes	14	4/7/2010	4/12/2011	382	79	25.8	Died—unknown cause
23	♂	No	1	4/9/2010	8/14/2011	424	78	15.9	Transmitter removed, snake released
24	♀	No	1	5/13/2010	12/1/2010	204	45		Transmitter failed early; found alive on 10/21/2013
25	♂	Yes	5	4/27/2010	10/11/2011	516	92	10.0	Lost—suspected transmitter failure ^c
26	♂	No	10	4/27/2010	12/30/2011	608	103	13.3	Not recaptured
27	♂	No	8	6/10/2010	12/30/2011	550	83	102.9	Not recaptured
28	♂	Yes	1	6/10/2010	10/18/2011	480	46	−2.6	Transmitter removed, snake released
29	♀	No	3	7/6/2010	6/15/2011	350	65		Lost—suspected transmitter failure ^c
30	♀	No	3	7/27/2010	8/23/2011	391	68	22.2	Transmitter removed, snake released
31	♂	Yes	0	8/5/2010	9/27/2011	423	62	23.1	Lost—suspected transmitter failure ^c
32	♂	Yes	4	9/29/2010	9/19/2011	357	53		Lost—suspected death by human action
33	♂	Yes	2	11/3/2010	10/24/2011	356	54	21.7	Transmitter removed, snake released

^a Indicates an LDT snake tracked previously as an SDT snake. ^b Snake initially translocated 519 m, but erratic movement patterns suggested translocation beyond the normal home range of females, so reassigned to the LDT group. ^c Transmitter failure suspected when a deteriorating signal was lost and circumstances did not suggest another cause. ^d Depredation suspected when the transmitter was found on the ground with no remains of snake nearby and no tooth marks on the transmitter.

2.5. Activity Range and Movements

We used R version 4.1.1 [72] and the package adehabitatHR version 0.4.19 [73] to calculate the activity area and movement parameters. Because we deliberately attempted to move LDT snakes outside of their normal home ranges and non-LDT snakes may have been moved outside their normal home ranges, we used the more generalized term “activity area” to describe space utilization. We used the calendar year for between-year comparisons, because the snakes became inactive during December and January. We calculated two activity area statistics for each snake for each calendar year of tracking: 100% minimum convex polygon (MCP) to facilitate comparison with previous studies and local convex hull (LCH) via the “adaptive sphere of influence” calculation [74,75]. We further

derived the mean daily movement (MDM) by dividing the distance moved between consecutive fixes by the number of days between fixes [76]. Since the number of location fixes affected the activity area estimates, we conducted a bootstrap analysis (10 randomly selected activity areas resampled 100 times each) to determine the minimum number of fixes needed for reliable estimates. Visual assessment of the bootstrapped curves suggested the need for at least 20 fixes.

For each location fix obtained for each snake, we calculated the distance to the nearest area with significant human modification (SHM). These areas were defined by the presence of buildings, roads, and well-maintained gardens and lawns (Figure 1). Areas subject to a lesser degree of human modification, such as plowed firebreaks and dirt trails, were not included. We obtained the UTM coordinates from Google Earth software (Google Inc., Mountain View, CA, USA) and calculated the Euclidean distances using R software.

2.6. Statistical Analyses

Because of legal constraints, only two snakes experienced no translocations, and many snakes experienced multiple SDTs. We therefore structured most of our analyses to include two groups of snakes—LDT and non-LDT—and treated the number of SDTs as a covariate.

2.6.1. Activity Area and Mean Daily Movement

We relied on linear mixed models (LMMs) to analyze the effects of LDT and SDT on activity areas and MDMs. Analyses were conducted using Jamovi 2.0.0 (The Jamovi Project, <https://www.jamovi.org>; accessed 9 February 2022) and the GAMLj library [77] with alpha set to 0.05. The GAMLj library calculated the marginal and conditional R^2 for mixed models. The marginal R^2 measures the variance explained by fixed factors and the conditional R^2 measures the variance explained by both fixed and random factors [78]. Prior to model fitting, data exploration was carried out following the protocol suggested by [79]. All models included sex and year as fixed factors and the number of SDTs and SVL as covariates. To account for activity area calculations of the same snake between years, we used snake identity as a random intercept in each model. Because of the relatively small sample sizes, we exercised care in choosing the interaction terms to include in the model. To maintain statistical power and minimize overfitting, we did not consider three-way or greater interactions, and only included two-way interactions if we found support for them in visualizations created during data exploration. As is common when using smaller datasets, two models showed a singular fit, which can sometimes indicate overfitting. However, such models can also be well defined and theoretically sensible [80]. Since our singular models generated results that largely agreed with the results from our other, non-singular models, we report them here.

We developed two sets of LMMs. The first set considered only the effect of the number of SDTs on non-LDT snakes. It included data from all years (2008–2011) and comprised three separate models with 100% MCP, 100% LCH, and MDM as the dependent variables in their respective models and the independent variables mentioned above (sex, year, SDTs, and SVL). The two-way interactions of sex \times year and sex \times SVL were also included. The second set of LMMs considered the effects of both LDT and SDTs on the activity ranges and movements. These models included both LDT and non-LDT snakes, but the data were limited to 2010 and 2011, because no LDT snakes were added to the study in 2008 and the two snakes assigned to the LDT group in late 2009 had insufficient location fixes (minimum of 20) to be included for that year. This second set of models also used the same dependent and independent variables as the first set, but included LDT (versus non-LDT) as a fixed factor and the interaction terms LDT \times year and sex \times SVL. We computed the estimated marginal means to characterize group differences.

2.6.2. Snake Mass and Mortality

To assess the effect of snake translocation on the body condition of recaptured snakes, we calculated the percent change between the initial and last recorded measures of mass. We used analysis of covariance (ANCOVA) with SPSS v. 23 (Statistical Package for the Social Sciences, Inc., Chicago, IL, USA) to test the effects of sex, LDT versus non-LDT groups, and the number of SDT translocations (covariate) on the percent change in mass, which was log natural-transformed to address positive skew and heteroscedasticity after adding a constant to make all values positive. We confirmed the homogenous regression slopes prior to analysis and computed partial eta-squared (η^2) as effect sizes.

We used survival analysis to examine snake mortality using R and the *survival* package version 3.2–11 [81]. We analyzed the data both considering and omitting human-associated mortalities. We calculated the survival rates using the Kaplan–Meier procedure [82] following Pollock et al. [83] and the guidelines of Robertson and Westbrooke [84]. The time period used in these calculations was the total number of days the snake was tracked. Tracking began when the snake was released into the field after transmitter implantation and ended upon the last fix obtained for the snake, whether at the end of the study, when found dead in the field, or when found ill in the field and subsequently taken into captivity. The number of days a snake was held in captivity for surgery or recovery was subtracted from the time period. Two snakes that died following surgical complications were excluded from this analysis. To examine the effect of translocation on mortality, we developed a Cox proportional hazard model [85] that included both the translocation group as a fixed factor and the number of SDTs as a covariate.

2.6.3. Risk of Human Conflict and Return to Capture Site after Translocation

We also utilized Cox proportional hazards models to address two questions related to the potential for renewed conflict with humans subsequent to translocation: does translocation affect (1) whether a snake returns to areas of potential human conflict and (2) whether it returns to areas near its original captured site?

To assess the first question (returning to the SHM area), we used a model that included the snake sex and translocation group as factors, and the distance from each snake's initial release point to the nearest SHM area as a covariate. The time period used as the dependent variable began when the snake was released subsequent to transmitter implantation and ended the first time that snake moved within 50 m of any SHM area, or upon the last fix obtained for the snake, whether at the end of the study, when found dead in the field, or when found ill in the field and subsequently taken into captivity. For snakes lost due to a presumed transmitter failure, the final date was calculated as the midpoint between the last fix and the subsequent date when looked for, but not found [86].

To assess the second question (returning near the original capture site), our model again treated the sex and translocation group as fixed factors, but this time we used the first SDT distance as the covariate. Only snakes that underwent at least one SDT from an area <50 m from an SHM area were used in this analysis, and only the first such event was considered to avoid pseudoreplication. This meant that the initial translocation of all snakes that underwent SDT immediately after transmitter implantation was included. Snakes in the LDT group or snakes that were not translocated after transmitter implantation were included if, subsequent to initial release, they moved into SHM areas and were then subjected to SDT. In such cases, only the first SDT event was included. We did not include the initial LDTs of those snakes in the LDT group in this analysis because, for several snakes in this group, the position of the SHM areas (i.e., residential development) blocked or would have significantly impeded their return to their original capture location in a large part because our protocol required that snakes moving into such areas be translocated back to areas they had been observed previously. The time period for this analysis began when the snake was released after SDT and ended when the snake returned within

50 m of the point it was translocated from or to the final location fix for that snake in the study, as defined above.

Since Cox proportional hazard models have few underlying assumptions [87], no transformations were applied to the data for any such analysis. We assessed the assumption of proportional hazard by using the proportional hazards test described by [88], as implemented in the *survival* package for R.

3. Results

A total of 30 adult *C. ruber* provided telemetry data at various periods of time between the middle of 2008 and the end of 2011. Because two of these snakes (snakes 2 and 11) were originally tracked as non-LDT, but were later re-assigned to the LDT group (becoming snakes 2.1 and 11.1; see above), our total sample size for the analyses was 32 (Table 1). The median number of days tracked for these snakes was 387.5 days (range: 11–1148), and a location fix was obtained for each of these snakes on average (\pm SD) every 5.6 ± 3.1 days. Of these snakes, 22 were placed in the non-LDT (SDT + NT) group (11 males and 11 females) and 10 were classed as LDT snakes (7 males and 3 females). Snakes returning to SHM areas were subjected to as many as 14 SDTs. Pooled location fixes (Figure 1) revealed that snakes were always found in areas with cover and avoided open areas, such as plowed fire breaks.

3.1. Activity Ranges and Movements

The results of the linear mixed models that included data from all years, but excluded LDT snakes, are shown in Table 2. These models provided mixed results for the effect of SDTs on activity areas. The model for 100% MCP, as the estimate for activity area, suggested that number of SDTs increased the activity range size (estimate = 0.56, 95% CI: 0.12–1.01, $p = 0.022$), whereas the model for 100% LCH did not (estimate = -0.14 , 95% CI: -0.34 – 0.07 , $p = 0.22$). The model that included MDM also showed a significant and direct effect of SDTs on snake movement (estimate = 1.93, 95% CI: -0.96 – 2.89 , $p < 0.001$). These models further suggested that sex influenced the activity area. The model using 100% LCH showed a direct effect of sex, with males having activity areas averaging 1.25 ha (186.5%) larger than females, when holding other variables constant (estimate = 1.25, 95% CI: 0.51–1.99, $p = 0.005$). Although the 100% MCP model did not show a primary effect of sex (estimate = 1.06, 95% CI: -0.45 – 2.57 , $p = 0.19$), the significant interaction between sex and SVL (estimate = 0.12, 95% CI: 0.02–0.22, $p = 0.033$) suggested that the male activity areas increased with SVL, whereas those of females remained relatively constant (Figure 2).

Table 2. Results of three linear mixed models examining the effects of the number of short-distance translocations (SDTs), sex, year, and snout–vent length (SVL) on activity ranges (100% minimum convex polygon (MCP) and 100% local convex hull (LCH)) and mean daily movements (MDM) of radiotransmitted adult Red Diamond Rattlesnakes (*Crotalus ruber*) during 2008–2011.

	100% MCP				100% LCH				MDM			
	F	Num df	Den df	p	F	Num df	Den df	p	F	Num df	Den df	p
SDTs	6.24	1	18.41	0.022	0.09	1	25.00	0.770	15.31	1	19.60	<0.001
Sex	1.90	1	15.69	0.187	5.66	1	25.00	0.025	0.01	1	16.99	0.927
Year	4.01	3	18.18	0.024	3.13	3	25.00	0.044	1.26	3	19.22	0.316
SVL	7.42	1	12.04	0.018	6.25	1	25.00	0.019	0.90	1	13.44	0.359
Sex \times Year	1.48	3	19.34	0.252	2.11	3	25.00	0.125	0.78	3	20.24	0.518
Sex \times SVL	5.72	1	12.97	0.033	2.67	1	25.00	0.115	1.84	1	14.39	0.196
R ² Marginal			0.61				0.55				0.52	
R ² Conditional			0.63				0.55				0.54	

Significant p -values are shown in bold. Sample sizes for males and females, respectively: 2, 4 (2008); 3, 8 (2009); 5, 5 (2010); 5, 4 (2011).

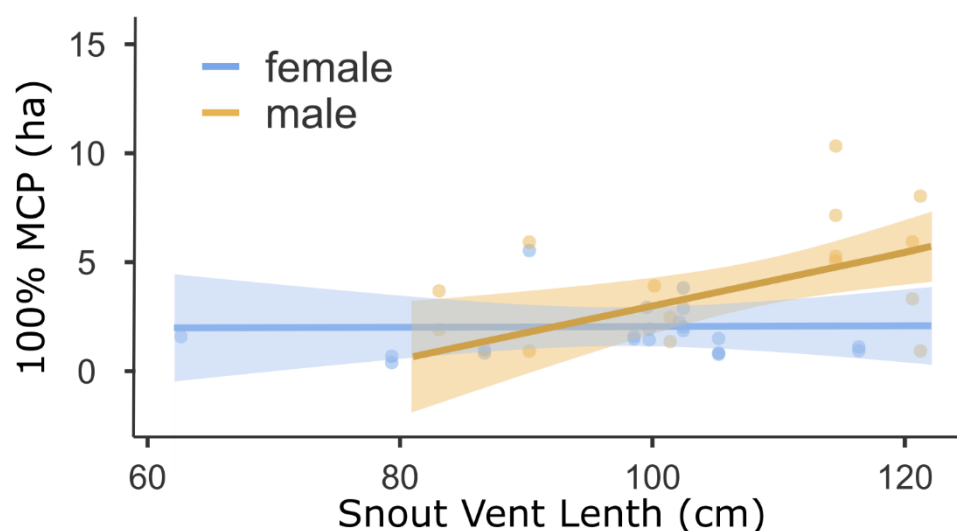


Figure 2. Model-adjusted relationships between snout–vent length and the 100% minimum convex polygon (MCP) activity area estimates for adult male ($n = 7$) and female ($n = 11$) Red Diamond Rattlesnakes (*Crotalus ruber*) that did not undergo long-distance translocation in Loma Linda, California. The 95% CI is shown around the trend lines.

The 100% LCH model also showed a significant and direct effect of SVL (estimate = 0.06, 95% CI: 0.02–0.11, $p = 0.018$). The year was significant in both the 100% MCP and 100% LCH models, with marginal means suggesting larger activity areas in 2009 compared to the other years, but with no obvious relationship involving precipitation (Figure 3) and despite the higher proportion of females (Table 2 footnote) tracked that year. For MDM, however, year exerted no significant effect.

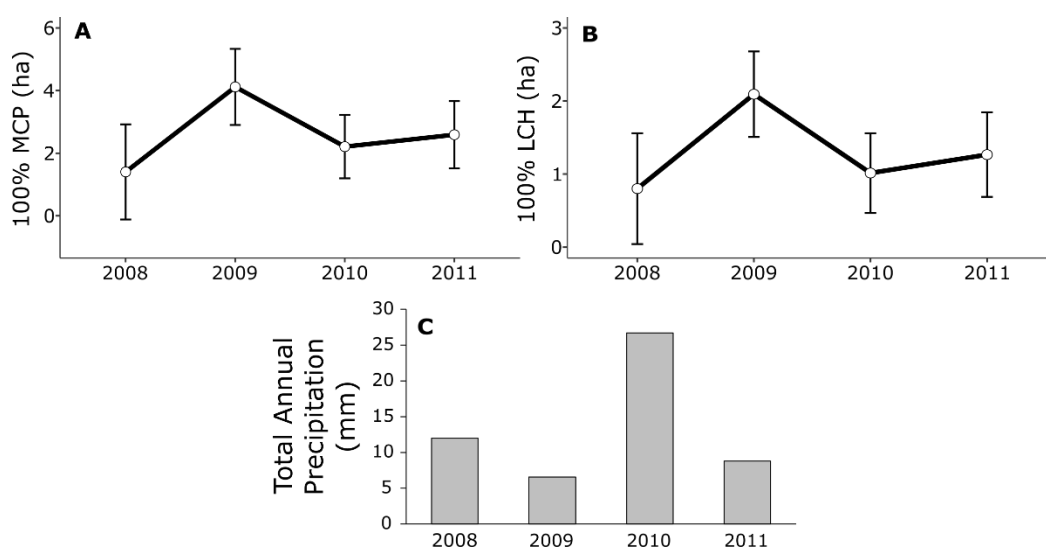


Figure 3. Estimated marginal means (\pm 95% CI) from the linear mixed models showing the activity areas per year as estimated using the (A) 100% minimum convex polygon (MCP) and (B) 100% local convex hull (LCH) for adult Red Diamond Rattlesnakes (*Crotalus ruber*) in Loma Linda, California. $n = 6, 11, 10$, and 9 , for 2008–2011, respectively. (C) Total precipitation, reflecting long-term drought, from the National Centers for Environmental Information weather station in the nearby Redlands, California, where the mean precipitation is 34.4 cm [67].

The results of the linear mixed models that considered LDT snakes, the number of SDTs, and only data from 2010 and 2011 revealed a clear effect of translocation type (LDT vs. non-LDT), especially in relation to the interaction with year (Table 3). All three models with the dependent measures 100% MCP, 100% LCH, and MDM showed this interaction

to be significant (respective estimates = 7.55, 95% CI: 3.42–11.68, $p = 0.001$; 2.43, 95% CI: 0.41–4.45, $p = 0.036$; and 8.64, 95% CI: 3.00–14.28, $p = 0.009$). Examination of the marginal means (Figure 4) indicated that, in the year LDT snakes were added to the study (2010), LDT snakes had activity areas 4.58 (100% MCP) and 3.47 (100% LCH) times larger than those of non-LDT snakes. The MDM distances were also 1.84 times larger in LDT snakes. However, these differences disappeared in the following year (2011). These models also provided mixed results regarding the effects of SDT on activity areas and MDM. The number of SDTs showed no significant effect on 100% MCP (estimate = 0.30, 95% CI: -0.05–0.64, $p = 0.10$), but was nearly significant for 100% LCH (estimate = 0.18, 95% CI: 0.01–0.36, $p = 0.052$). The effect of SDTs was significant and directly related to MDM (estimate = 0.76, 95% CI: 0.25–1.27, $p = 0.007$). Unlike the previous models, all models showed a significant effect of sex (100% MCP: estimate = 3.00, 95% CI 0.89–5.12, $p = 0.010$; 100% LCH: estimate = 1.31, 95% CI 0.20–2.42, $p = 0.047$; MDM: estimate = 6.24, 95% CI 2.91–9.58, $p = 0.004$), with males exhibiting larger activity areas and greater MDM than females, with males averaging 3.00 ha (82.6%) larger for 100% MCP, 1.31 ha (98.5%) larger for 100% LCH, and 6.24 m/d (88.9%) larger for MDM.

Table 3. Results of the omnibus tests from three linear mixed models examining the effects of long-distance translocation (LDT vs. non-LDT), the number of short-distance translocations (SDTs), sex, year, and snout–vent length (SVL) on the activity ranges (100% minimum convex polygon (MCP) and 100% local convex hull (LCH)) and mean daily movements (MDM) of adult *Crotalus ruber* during 2010 and 2011.

	100% MCP				100% LCH				MDM			
	<i>F</i>	Num df	Den df	<i>P</i>	<i>F</i>	Num df	Den df	<i>P</i>	<i>F</i>	Num df	Den df	<i>P</i>
LDT	21.28	1	25.00	<0.001	7.17	1	9.14	0.025	3.07	1	11.62	0.106
SDTs	2.90	1	25.00	0.101	5.39	1	8.35	0.052	13.46	1	10.77	0.007
Sex	7.74	1	25.00	0.010	3.72	1	12.33	0.047	9.12	1	14.41	0.004
Year	10.51	1	25.00	0.003	0.13	1	8.57	0.077	0.03	1	11.00	0.009
SVL	0.27	1	25.00	0.608	4.17	1	24.02	0.727	8.64	1	24.69	0.856
LDT × Year	12.82	1	25.00	0.001	5.58	1	12.25	0.036	9.02	1	14.33	0.009
Sex × SVL	0.37	1	25.00	0.547	0.55	1	9.12	0.475	0.54	1	11.61	0.477
<i>R</i> ² marginal			0.64				0.47				0.59	
<i>R</i> ² conditional			0.64				0.52				0.66	

Significant *p*-values are shown in bold. Sample sizes: 7 LDT and 6 non-LDT males, 2 LDT and 6 non-LDT females (2010); 7 LDT and 5 non-LDT males, 2 LDT and 4 non-LDT females (2011).

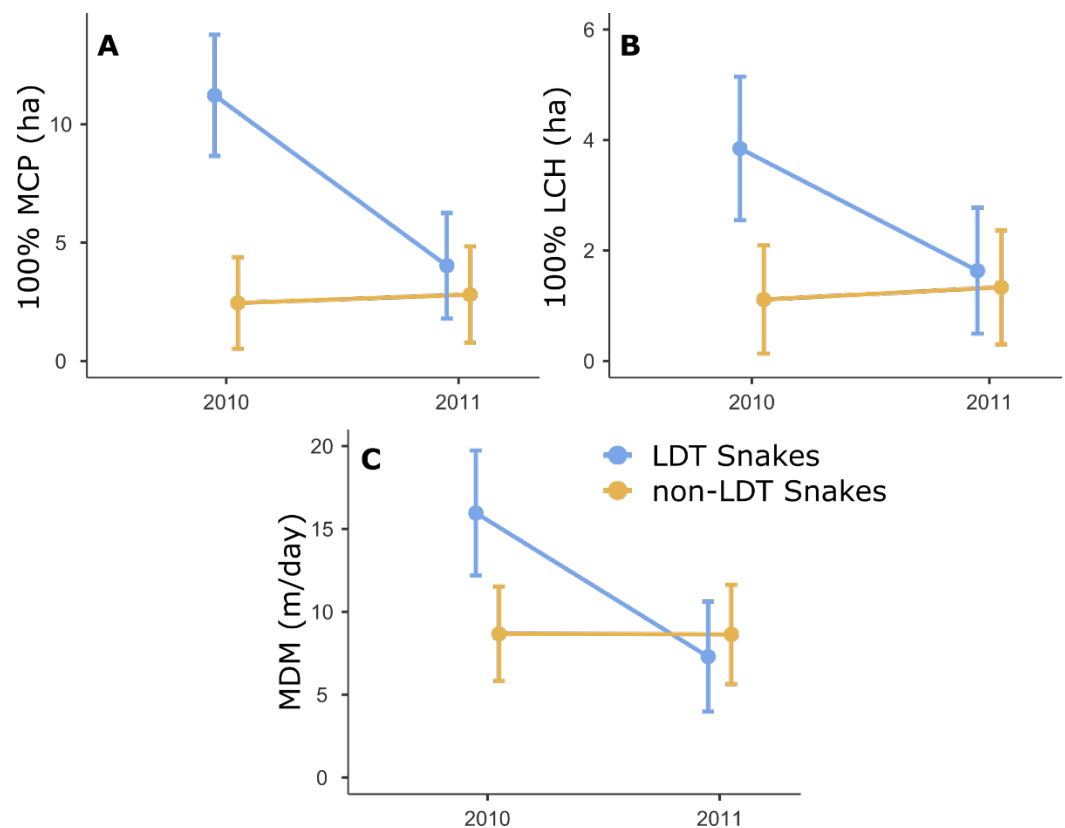


Figure 4. Estimated marginal means ($\pm 95\%$ CI) from the linear mixed models showing the interaction of long-distance translocation (LDT) and year on the activity area as estimated using the (A) 100% minimum convex polygon (MCP) and (B) 100% local convex hull (LCH), and (C) mean daily movement (MDM) for adult Red Diamond Rattlesnakes (*Crotalus ruber*) in Loma Linda, California. $n = 6$ LDT and 10 non-LDT in 2010, and 8 LDT and 9 non-LDT in 2011. Snakes subjected to LDT in 2010 exhibited greater activity areas and movements than in 2011.

3.2. Snake Mass and Mortality

We measured the change in mass of 19 recaptured snakes (including both sampling periods for snake 11). The body mass change ranged from 35.2% loss to 100.9% gain (Table 1). Thirteen (68.4%) of the 19 individuals gained mass, including 10 of 12 males and 3 of 7 females (Table 1). The ANCOVA model revealed no difference in the percent mass change between the sexes (mean \pm SE: males $18.6\% \pm 8.5\%$ gain, $n = 12$; females $3.1\% \pm 10.4\%$ loss, $n = 7$; $F_{1,14} = 0.32$, $p = 0.58$, partial $\eta^2 = 0.02$), no difference between LDT groups (LDT $17.7\% \pm 4.0\%$ gain, $n = 12$; non-LDT $6.5\% \pm 10.6\%$ gain, $n = 7$; $F_{1,14} = 0.96$, $p = 0.34$, partial $\eta^2 = 0.06$), no effect of the number of SDTs (range 0–16; $F_{1,14} = 0.65$, $p = 0.43$, partial $\eta^2 = 0.05$), and no interaction between sex and LDT group ($F_{1,14} = 0.66$, $p = 0.43$, partial $\eta^2 = 0.05$). All effect sizes were similarly small.

Based on the available evidence, we determined that nine deaths occurred during the study (Table 1). Two events resulted from complications associated with surgery. One of these two (snake 5) died during transmitter replacement surgery. The other (snake 10) was tracked for 88 days, but then sustained an injury that reopened the surgical incision and caused tearing, exposing a large portion of the coelomic cavity. The snake died four days later in our laboratory, despite our best efforts to disinfect and close the wound. Of the seven remaining deaths, we attributed two to predation. We found the transmitter of snake 4 on open ground with unambiguous bite marks, and near a portion of the snake's rattle containing the painted segments used for identification. We found the transmitter of snake 14 on the ground with probable bite marks, but without snake remains nearby. We attributed three deaths to the action of humans. We found the decapitated body of snake 2.1 in a plowed firebreak area 30 m from a home and a private tennis court. The

clean nature of the decapitation wound and absence of injury to the remaining body suggested that a sharp object was used followed by burial of the head, which was not found. Snake 20 was buried by heavy earthmoving equipment as part of a landscaping project to expand the cemetery in the western portion of the study site. We confirmed this death by digging up the snake's remains. A third presumed case of human-caused mortality resulted when snake 32, observed in a large pile of brush and rocks within the area of the cemetery landscaping project nine days after SDT away from the same landscaping project, disappeared after the pile was loaded by heavy equipment into large dumpsters and hauled away. In the remaining two cases of death, one resulted from apparent disease and the other from unknown causes. We found snake 17 writhing and biting the ground in an area of coastal sage scrub, and subsequently euthanized the snake when it deteriorated further in our lab. We found the transmitter of snake 22 devoid of marks and in a large brush pile 24 m from a house, suggesting either predation or human-caused death. A summary of first-year survival is shown in Table 4.

Table 4. Summary of first-year survival (≤ 365 days of tracking) for adult *Crotalus ruber* that were either long-distance translocated (LDT) or not (non-LDT). Survival rate excludes snakes lost during the study from presumed transmitter failure and one snake that died of surgical complications during the first year of tracking.

Group	N	Survived (%)	Lost (%)	Confirmed Dead (%)	Survival Rate (%)
Without Human Mortality					
Non-LDT	21	61.9	28.6	9.5	86.7
LDT	9	88.9	11.1	0.0	100.0
With Human Mortality					
Non-LDT	21	61.9	28.6	9.5	86.7
LDT	10	80.0	10.0	10.0	88.9

We tracked all snakes for a total of 13,616 days, which corresponded to 37.30 snake years. The minimum annual mortality based on snake years was 2.7% (one event) for disease, 5.4% (two events) for predation, and 8.0% (three events) for human-associated causes. Including the presumed predation/human-caused death of snake 22, the combined mortality for predation and human causes was 16.1% (six events) and the total annual mortality was 18.8% (seven events). These calculations excluded the two surgery-related deaths.

We conducted two survival analyses classifying each of the snakes above as ending in a mortality event. The first analysis included human associated deaths. The mean (\pm SE) survival time for all snakes was 853 ± 94 days, with 857 ± 139 days for LDT snakes and 858 ± 121 days for non-LDT snakes. The mean survival time was 808 ± 136 days for males and 894 ± 126 days for females. Cox proportional hazard analysis failed to detect significant effects of LDT, sex, or number of SDTs on survival (LDT hazard ratio (HR) = 1.30, 95% CI = 0.26–6.41, $z = 0.32$, $p = 0.75$; sex HR = 1.04, 95% CI = 0.21–5.15, $z = 0.05$, $p = 0.96$; SDTs HR = 0.95, 95% CI = 0.79–1.14, $z = -0.52$, $p = 0.61$). The second analysis excluded human associated deaths. For this analysis, the survival time for all snakes was 974 ± 77 days, with 1036 ± 101 days for LDT snakes versus 946 ± 103 days for non-LDT snakes, and 981 ± 106 days for males versus 962 ± 116 days for females. The Cox proportional hazard analysis for this group again failed to detect a significant effect of LDT, sex, or number of SDTs (LDT HR = 0.54, 95% CI = 0.51–5.63, $z = -0.52$, $p = 0.60$; sex HR = 1.06, 95% CI = 0.13–8.68, $z = 0.05$, $p = 0.96$; SDTs HR = 1.00, 95% CI = 0.80–1.26, $z = 0.03$, $p = 0.98$).

3.3. Risk of Return to Human-Modified Areas

Following transmitter implantation, snakes (including those from both translocation groups) were initially released an average of 152.5 m (range: 25.9–459.5 m) away from the nearest SHM area. Omitting two snakes initially released <50 m away from SHM areas,

73.3% of all snakes (22 out of 30), regardless of translocation group, moved to areas within 50 m of SHM areas subsequent to initial release. The median time for these snakes to move to these areas was 48 days (95% CI = 19–261) based on a Kaplan–Meier analysis. Cox regression revealed that an increase in distance between a snake’s release point and SHM area reduced the risk of a snake returning to such areas (HR = 0.989, 95% CI = 0.978–0.999, $n = 30$, $z = -2.09$, $p = 0.037$). While holding other factors constant, every 1 m increase in distance from the release point to SHM areas decreased the risk of returning to such areas by 1.2% (95% CI = 0.1–2.2%). However, no difference was detected between the translocation groups (HR = 95% CI = 0.59–3.67, $n = 30$, $z = 0.82$, $p = 0.41$) or sexes (HR = 0.74, 95% CI = 0.30–1.84, $n = 30$, $z = -0.65$, $p = 0.52$).

3.4. Risk of Return to Area of Capture after Translocation

Of the 22 snakes that experienced SDT away from SHM areas at some point during the study, the first such translocation for these snakes averaged (\pm SD) 246.2 \pm 155.7 m (range 32.2–633.3 m). Omitting one snake that was translocated less than 50 m, 11 of 21 (52.4%) returned to within 50 m of their original location. The median time to return was 163 days (95% CI = 31–no upper limit) based on Kaplan–Meier analysis. Cox regression again showed a small, but significant, effect of the distance the snake was translocated away from its capture site ($n = 21$, HR = 0.984, 95% CI = 0.973–0.995, $z = -2.78$, $p = 0.005$). Keeping other variables constant, for every 1 m increase in the translocated distance, the risk of return decreased by 1.6% (95% CI = 0.5–2.7%). No differences existed between the translocation groups (HR = 1.466, 95% CI = 0.283–7.601, $z = 0.46$, $p = 0.65$) or sexes (HR = 0.367, 95% CI = 0.086–1.567, $z = -1.35$, $p = 0.18$).

None of the 10 LDT snakes returned to within 50 m of their initial capture sites, except for the one female (snake 19) that was initially translocated 519 m on 13 October 2009 but was assigned to the LDT group due to its extensive and erratic movements after translocation. This snake returned to within 50 m of its initial capture site after 184 days. Another LDT snake (snake 33), translocated 2573 m from his initial capture site, appeared to make an effort to return. Subsequent to its initial release on 1 November 2010, this snake moved 681 m in a direction toward its capture site until 11 November 2010, when it moved into a residential area and on the grounds of an elementary school. It was then translocated 633 m back to its original translocated position. The snake again moved 618 m in a direction towards its capture site and returned to within 126 m of the same elementary school on 15 December 2010. At this point, to prevent the snake from returning to the elementary school, we broke protocol and again recaptured the snake prior to re-entering an area of potential human conflict (which is why this translocation was excluded from the translocation analysis above). We translocated this snake 582 m (straight-line distance) back to the point of its initial release. It then overwintered near this release point. The snake did not move in the direction of its capture location the following spring and was found paired with a female on 3 March 2011.

4. Discussion

Mitigation translocation has received increasing attention as an option for dealing with nuisance wildlife, including venomous snakes. However, three key concerns have been raised: (1) the potential of harm to the translocated snake; (2) return of the snake to the original site of human–snake conflict; and (3) population-level effects that result from the translocated animal. In this study, we used radiotelemetry to assess the effects of LDT and SDT on adult rattlesnakes to improve our understanding of the first two concerns. If translocation represents a successful management tool for reducing human–snake conflict, it should minimally impact the translocated snake while reducing the likelihood of the snake returning to a site of potential conflict. We sought to learn how the distance of nuisance snake translocation from SHM areas would impact their subsequent spatial ecology, movements, body condition, survival, and, ultimately, their potential for conflict with humans. Our method of analysis allowed us to draw useful conclusions, despite our

study design being constrained by property owner requests and liability issues that compelled us to translocate all snakes initially found in SHM areas, and those that returned subsequently to these areas.

4.1. Translocation Effects on the Snake

One major concern about mitigation translocation is the potential for negative impacts on the snake. Previous studies suggest that translocated snakes are prone to wander and exhibit increased stress levels, which may ultimately lead to increased mortality (see Introduction). Consistent with these studies, we found evidence that both SDT and LDT increased the activity range size and mean daily movement. Although the results of our statistical models were mixed for the effect of SDTs, some of these models suggested an increase in activity range size of 0.18–0.56 ha per SDT and an increase in MDM of 0.76–1.93 m per SDT. The effect of LDT (vs. non-LDT) was much clearer, with the models suggesting a 3.47–4.58-fold increase in the activity area and a 1.84-fold increase in MDM for LDT snakes compared to non-LDT snakes during their first year after translocation. However, our results also showed that the activity areas and MDMs of LDT snakes were similar to those of non-LDT snakes in the second year after translocation. The difference between years suggests that these snakes became acclimated to their new environment [59].

Our results further showed males occupying activity ranges 1.25–3.00 ha (82.6–186.5%) larger than those of females, and moving up to 6.24 m/d (88.9%) more than females. We expected these differences, as males of *C. ruber* elsewhere [49] and those of other rattlesnake species (e.g., [89–93]; but see [94]) exhibit greater levels of activity than females. Moreover, the activity range size increased with increasing SVL for male snakes, but not for female snakes. We did not detect or explicitly test interactions between sex and LDT or SDTs, but sex- and size-based differences may exist in the behavior of snakes translocated to unfamiliar surroundings and, ultimately, in their tolerance to LDT. Because males roam widely when searching for females, they may be equipped with behavioral and physiological adaptations that enable them to navigate and otherwise cope with being in previously unexplored areas, which females, who generally move much less and have smaller home ranges, may lack. The presence of such physiological adaptations has been suggested in several field studies [28,61,62]. Although only male rattlesnakes were used in the studies, snakes repeatedly subjected to SDT developed larger medial cortexes than the controls, presumably in response to increased navigational demands [61,62], and the increased testosterone levels in LDT snakes may aid in spatial learning and memory [28]. The studies further found no differences in the levels of the stress hormone corticosterone between translocated and control snakes. If males are adapted to cope with unfamiliar areas, then such a reduced stress response would be expected.

Although our snakes exhibited increases in space use and movements due to both LDT and SDTs, the changes in body condition and survival (overall and during the first year) were similar between the sexes, between LDT and non-LDT snakes, and unaffected by the number of SDTs. Prior research has shown no differences in mortality for SDT snakes compared with controls [49,50,60–62]. For LDT snakes, however, previous studies offer mixed conclusions. Brown et al. [49] did not detect a difference in mortality between LDT and non-translocated *C. ruber*, but other studies of *C. atrox* and *C. horridus* reported that LDT snakes suffered higher mortality [48,59]. (Another study [28] observed no mortality in both control and LDT snakes, but the study duration was only one month.) The difference between *C. ruber* and other species may be due to differences in habitat and/or dependence upon specific hibernacula for overwinter survival. In cooler climates, snakes unable to find suitable locations to hibernate (\approx brumate) are much less likely to survive the winter [37]. Indeed, a significant number of mortalities among LDT snakes of *C. horridus* [59] occurred during the winter, and high winter mortality was reported in repatriated Massasauga rattlesnakes (*Sistrurus catenatus*) [54,56]. In warmer climates, such as

lower elevations in southern California, the need to utilize specific or communal hibernacula to escape freezing conditions is reduced or absent [64,95], and hence overwintering may have less of an effect on survival.

Regardless of translocation experience, our study subjects experienced human-associated mortality (8.0%/year) at the same rate as natural causes (2.7% for disease, 5.4% for predation, 8.0% combined). Without the agreements in place with property owners and our Herculean translocation efforts (122 translocations away from SHM areas), these snakes would likely have experienced substantially higher mortality. Clearly, snakes at the suburban–wildlands interface suffer inevitably high risks of mortality.

4.2. Risks Associated with Human–Snake Conflict

The second major concern of mitigation translocation is whether the snake is less likely to return to the area of potential human–snake conflict. We considered two measures of potential conflict in relation to snake translocation: (1) whether snakes returned to SHM areas in general, and (2) whether snakes returned to the areas near their original capture sites. Prior studies of snake translocation have only considered the latter measure.

A high proportion (73.3% of 30) of snakes moved near SHM areas at some point during the study (median of 48 d after initial release), and roughly half of those translocated a short distance away from SHM areas (52.4% of 22) returned to within 50 m of their original capture site in an SHM area (median of 163 days). The probability of return to either SHM areas or the original capture site did not differ among translocation groups or sexes. Some snakes in all groups were subjected to SDTs, so the lack of differences between translocation groups seems expected. However, the risk of a snake moving to an SHM area or returning to the original site of capture decreased by approximately 1.2% and 1.6%, respectively, per 1 m translocated distance. Clearly, the capacity of translocation to reduce conflict depends on the distance a snake is moved from the location of conflict.

Snakes subjected to LDT may nevertheless experience negative impacts. Such individuals may take time to orient themselves to the new environment and, as a result, increase their movements and exposure to risks as they search for suitable areas to forage, bask, shelter, and locate mates. If these snakes exhibit natal habitat preference induction and have established natal home ranges that include SHM areas, then such snakes may seek such areas once translocated, and either come into conflict with humans again, or move into sub-optimal habitats that the snake perceives to be similar to SHM areas, and thereby increase their risk of mortality [96].

4.3. Implications for Managing Nuisance Rattlesnakes

Those who deal with human–wildlife conflict must take into consideration the three aforementioned issues when mitigating situations involving nuisance animals. Our research has addressed the first two issues for rattlesnakes, which include the potential negative impact to the individual nuisance animal and the risk to humans (or property) posed by a returning animal. The third issue is the potential negative impact to the population the animal is a part of and/or the population it may be moved to if translocated. We will comment on each of these as they relate to managing nuisance rattlesnakes.

With regard to the welfare of the nuisance animal, there are three major options for dealing with nuisance rattlesnakes: (1) leaving the snake alone, which a property owner often objects to; (2) euthanasia, which has the most deleterious impact to the snake and is therefore considered least humane; or (3) removal of the live snake, either by translocating it to another area or maintaining it indefinitely in captivity. For translocation, a trade-off exists between immediate effects on the snake’s behavior, including an increased risk of death (the major problem with LDT), versus future return to the area of conflict (the major problem with SDT), which could result once again in human conflict and the death of the snake. Long-distance translocation has been strongly criticized as a strategy that unacceptably increases the probability of snake death (e.g., [13,48,59]). However, two studies of *C. ruber* (ours and [49]) suggest that LDT can be a viable option for at least some species,

or for snakes in certain climates or habitats. Much of the mortality reported for translocated snakes of other species has been associated with brumation \approx hibernation [56,59], often at communal hibernacula. Repatriated snakes (captive-raised prior to release in the wild) have similarly been especially vulnerable during the hibernation period [54]. The milder climate of southern California, where many snakes overwinter individually without strong site fidelity [64,95], may reduce the risk of overwintering mortality in translocated snakes. Other factors no doubt contribute to translocation success, including the species' biology (*C. ruber* is a relatively sedentary species [64]), snake population density, and availability of prey and refugia. At present, we find no compelling evidence to recommend against LDT in the southern California region, except at higher altitudes where communal overwintering at scarcely distributed suitable sites may be critical for survival. Nevertheless, we certainly agree with others (e.g., [13,18,97–99]) that public education about tolerating nuisance rattlesnakes would be a viable alternative or supplement to mitigation translocation.

Although LDT may increase the probability of rattlesnake mortality in the short term, at least the snakes are given a chance to succeed. Some consider the reduced survival rate of LDT unacceptable (e.g., [13,59]); however, all wild snakes will experience death eventually through illness, starvation, depredation, and/or senescence, any of which might cause equal levels of suffering [100]. Many LDT snakes live beyond the first year of highest vulnerability, and thereafter may thrive as successfully as non-translocated snakes [59]. We see no reason why LDT would be more unethical than euthanasia, particularly in areas where SDT or tolerance are not suitable options for property owners.

With regard to the risk of the nuisance animal to humans or property, venomous snakes actually pose a very low risk to humans in the United States. Recent estimates put the incidence of snake envenoming at 0.79 per 100,000 per year and the incidence of death at 0.001 per 100,000 per year [40]. Certainly, the risk is higher for those who live in more rural areas, those who spend significant time in natural areas for recreational or occupational purposes, and those whose health may be somewhat compromised. Yet, in many cases, human envenomation occurs because a human deliberately chooses to interact with the snake—either to harass, kill, or capture it—suggesting that the risk of envenomation would be significantly reduced if people would simply choose to leave the snake alone.

Although no research has examined the third issue for rattlesnakes, strategies for mitigating human–wildlife conflict can be expected to exert effects at the population level [11,13,16,34,35]. Certainly, indiscriminate use of euthanasia has the potential to deplete local populations—an outcome that can be particularly undesirable if the species in question is protected, as in our study, or is a high-trophic-level consumer (i.e., predator), which can lead potentially to profound ecosystem change [13,45,46]. Moreover, euthanasia may alter sex ratios by affecting one sex more than the other. Previous studies indicate a male bias in snake mortality caused by humans [101,102], and male rattlesnakes may be responsible for more human envenomations than females [103], suggesting that males may be more likely to come into conflict with humans.

Translocations involving substantial distance have the potential to affect both the source population (assuming an absence of homing to the original location) and the population the animal is moved to. For rattlesnakes, LDT beyond the typical home range, but within a few kilometers beyond it, involves distances too limited to affect anything more than the immediate neighbors of the translocated snake. Given the dynamic nature of snake home ranges, which contract and expand seasonally and from year to year, and generally overlap widely the ranges of other snakes [104], any impacts from the translocation of a few snakes should be fairly negligible. More problematic would be the removal of an excess number of snakes from a given location, as the local population could suffer predator depletion. Sex ratios might also become skewed in both the source (female-biased, with the removal of more males) and receiving (male-biased) populations. These risks are not only dependent on the distance these snakes are moved, but also on the number of animals moved. Nuisance snake dumping involving dozens of individuals at the

same location has been described in Arizona [38], and no doubt has negative repercussions for the dumped snakes and the local environment. With regional translocation beyond the local deme, the translocated snake may become a vector of disease transmission to the receiving population, alter the genetic structure of the receiving population, or increase the receiving population beyond its carrying capacity [11,45]. For rattlesnakes, the consequences of translocation into currently unoccupied areas or beyond the species' range have not been examined, but there are compelling reasons to recommend against this practice, unless it is part of a carefully monitored repatriation program ([56] and references therein).

5. Conclusions

This study investigated nuisance snake translocation as a management tool for reducing human–snake conflict. Although rattlesnakes translocated beyond their normal home range exhibited increased space use and movements, those moved greater distances from human–modified areas were less likely to return, and they experienced survival rates similar to those moved short distances. Thus, our findings add to the growing body of evidence that translocation of nuisance snakes can be a viable approach to reduce human–snake conflict, at least for some species and/or locations. Despite accumulating studies on the effects of translocation on snakes, the factors that influence successful implementation remain unclear and warrant continued investigation. We therefore urge caution in generalizing. Studies vary substantially in their translocation protocols, duration, and assessments of behavior, physiological impacts, and mortality, and all are constrained by relatively small samples.

Supplementary Materials: The following are available online at: www.mdpi.com/article/10.3390/d14020130/s1. Table S1: Rattlesnake telemetry data. Table S2: Codebook for rattlesnake telemetry data.

Author Contributions: A.G.C. and W.K.H. contributed to the conceptualization, study design, and writing, though A.G.C. conducted almost all of the data collection, data curation, and statistical analyses. Both authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available in the attached Supplementary Files.

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Conflicts of Interest: The authors declare no conflict of interest.

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