

MANAGEMENT OF RATTLESNAKE-HUMAN INTERACTION: THE EFFECTS OF
SHORT-DISTANCE TRANSLOCATION ON *CROTALUS O. OREGANUS*

A Thesis

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The Faculty of Graduate Studies

of

The University of Guelph

by

JEFFERY ROBERT BROWN

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ABSTRACT

MANAGEMENT OF RATTLESNAKE-HUMAN INTERACTION: THE EFFECTS OF SHORT-DISTANCE TRANSLOCATION ON *CROTALUS O. OREGANUS*

Jeffery Robert Brown
University of Guelph, 2006

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Professor Ronald J. Brooks

Short-distance translocation (SDT) is commonly used to mitigate rattlesnake-human interaction, yet little is known about the success rate, nor the effects of translocation on the spatial ecology, behaviour, and welfare of rattlesnakes. Because rattlesnakes demonstrate homing behaviour, I predicted that after SDT snakes would return to capture locations, which would increase rattlesnake movements and activity range size and ultimately have negative effects on body condition, behaviour, and mortality rates. I used radio-telemetry to monitor 28 Western Rattlesnakes (*Crotalus o. oreganus*) near Osoyoos, BC in 2004 and 2005. Forty seven 500m SDTs were performed on 14 translocated individuals. Translocated rattlesnakes moved further than control rattlesnakes but there was no evidence of an effect on frequency of movements or size of activity ranges. Although SDT snakes moved further, there was no evidence body condition, behaviour, or mortality rates were affected by SDT. SDT was a viable short-term solution to rattlesnake-human interaction but failed as a stand alone long-term management strategy due to high rates of return.

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	i
LIST OF TABLES.....	v
LIST OF FIGURES.....	vi
INTRODUCTION	1
General Introduction	1
Effects of Short-distance Translocation	3
Short-distance Translocation as a Management Tool	4
MATERIALS AND METHODS	6
Study Methods	6
a. Study Site	6
b. Radio-Telemetry	8
<i>Radio-Transmitter Implantation</i>	8
<i>Radio-Tracking</i>	9
c. Experimental Translocation	9
Statistical Methods	11
a. Data Analyses	11
b. Statistical Analyses	11
c. Movement Pattern Analyses	12
<i>Full Season Movement Pattern Analyses</i>	13
<i>Seasonal Movement Pattern Analyses</i>	13
d. Activity Range Analyses	14
e. Condition Analyses	15
f. Behaviour Analyses	15
g. Multiple Translocation Analyses	16
RESULTS	18
Effects of Short-distance Translocation	19
a. Full Season Movement Patterns	19
<i>Total Distance Moved</i>	19
<i>Rate of Movement</i>	19
<i>Frequency of Movement</i>	22
b. Seasonal Movement Patterns	22
<i>Total Distance Moved</i>	22
<i>Rate of Movement</i>	23
<i>Frequency of Movement</i>	28
c. Activity Range	28
<i>Range Length</i>	28
<i>Range Width: Range Length</i>	31
<i>Minimum Convex Polygon</i>	31
d. Condition	32

e. Behaviour	32
<i>Mating Success</i>	32
<i>Frequency of Exposure</i>	32
<i>Habitat Use</i>	36
f. Mortality	36
Short-distance Translocation as a Management Tool	38
a. Full Season Short-distance Translocation	38
<i>Success Rate of Short-distance Translocation</i>	38
<i>Multiple Translocations</i>	38
<i>Site Fidelity</i>	38
b. Seasonal Short-distance Translocation	40
<i>Success Rate of Short-distance Translocation</i>	40
<i>Multiple Translocations</i>	40
DISCUSSION	43
Effects of Short-distance Translocation	43
a. Movement Patterns and Activity Range	43
b. Condition, Behaviour, and Mortality	47
Short-distance Translocation as a Management Tool	50
a. Success Rate	50
b. Multiple Translocations	52
Conservation and Management Implications	53
Conclusions	56
LITERATURE CITED	57
APPENDIX A	63
APPENDIX B	64
APPENDIX C	65

LIST OF TABLES

Table 1: Mean full season movement pattern values, with standard deviations, for Western Rattlesnakes in control and translocation treatments..	20
Table 2: Mean full season activity range values, with standard deviations, for Western Rattlesnakes in control and translocation treatments.....	30
Table 3: Summary information for 14 translocated rattlesnakes, with standard deviations, over the full season and by dispersal, mating, and ingress seasons.....	39
Table A1: Sample size information for 23 individual rattlesnakes representing 28 full active seasons included in the short-distance translocation analyses	63
Table B1: Summary of the year, location, and cause of 25 Western Rattlesnake mortalities on the study site, collected between April 2004 and October 2005	64
Table C1: Power analysis for all variables and their statistical tests included in the short-distance translocation data analyses. Power values are based on the ability to detect a 'large' effect size following the methods of Cohen (1977) and an alpha of 0.05.....	65

LIST OF FIGURES

Figure 1: Map of the study site, and its location in British Columbia, including the locations and types of anthropogenic developments, and experimental translocation and control treatments.	7
Figure 2: Linear regression of the total distance moved (TDM), in meters, over the full active season on the number of translocations per individual.	21
Figure 3: Comparison of the mean total distance moved (TDM), in meters, with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments by season.....	24
Figure 4: Linear Regression of the total distance moved (TDM), in meters, on the number of translocations per individual during the dispersal season.	25
Figure 5: Comparison of the movement rate, measured in mean distance per movement (MDM), with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments by season..	26
Figure 6: Linear regression of the movement rate, measured in mean distance per movement (MDM), on the number of translocations per individual in the dispersal season.....	27
Figure 7: Comparison of the mean number of movements per day (NMD), with 95% confidence intervals, for Western Rattlesnakes in the control and translocation treatments by season.....	29
Figure 8: Log-log linear regression of mass on snout-vent length of 222 individual Western Rattlesnakes captured between April 2004 and October 2005.....	33
Figure 9: Comparison of the mean body condition, with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments by season.....	34
Figure 10: Comparison of the mean percent of telemetry locations where rattlesnakes were found basking, concealed, or moving, with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments.....	35
Figure 11: Comparison of the mean percent of telemetry locations, with 95% confidence intervals, in the five major habitat types on the study site for Western Rattlesnakes in control and translocation treatments.	37
Figure 12: Frequency distribution of the distance from the previous capture location in an area of human activity, in 50m intervals, for unsuccessful translocation events.....	41

INTRODUCTION

General Introduction

Intensive development throughout the Western Rattlesnake's (*Crotalus oreganus oreganus*) range has led to an increase in rattlesnake-human interactions. Because rattlesnakes are venomous, they are perceived as potentially dangerous when they interact with human populations (Hardy *et al.* 2001; Nowak *et al.* 2002), and therefore, face intentional and accidental mortality in areas of human activity (Seigel 1986; Brown 1993; Bonnet *et al.* 1999). Management strategies directed toward human safety and rattlesnake conservation need to be developed to mitigate rattlesnake-human conflict. Translocation is gaining popularity across North America as a tool to minimize the risk to both rattlesnakes and humans where they interact (Nowak 1997; Sullivan *et al.* 2004).

Translocation is a common conservation and management technique, which has traditionally been applied to establish, reestablish or augment wildlife populations (Griffith *et al.* 1989; Burke 1991; Dodd and Seigel 1991; Reinert 1991; Bright and Morris 1994; Wolf *et al.* 1996; Fischer and Lindenmayer 2000). More recently, translocation has been applied to wildlife-human conflict to avoid the killing of animals considered a threat to humans (Reinert and Rupert 1999). The translocation of problem animals can solve an immediate conflict with human populations (Blanchard and Knight 1995; Shine and Koenig 2001), but little attention has been paid to the effects such practices may have on snakes or to the long-term success rates of these measures.

Two 'types' of translocation have been applied to solve rattlesnake-human conflict; long distance translocation (LDT) and short-distance translocation (SDT). In LDT, individuals are moved to an area outside the known or estimated home range of the

animal. In SDT, an individual is moved to a location within or very close to its estimated or known home range, and thus might be expected to return to the original site. Whether the translocation occurs over a long distance or a short distance; the ultimate goal is to remove the perceived threat to human safety, ensure the survival of the animal, and prevent the animal's recurrence as a nuisance (Sealy 1997).

Most past research on translocation of snakes has focused on LDT. Although LDT may reduce rattlesnake-human conflict, this technique may result in negative effects on snake populations. Because the translocated individual will be released in a novel environment, researchers must ensure individuals are released in an area that can meet the snake's biotic and abiotic requirements (Dodd and Seigel 1991; Reinert 1991). In addition, negative effects associated with disease transfer (Cunningham 1996; Shine and Koenig 2001; Seigel and Dodd 2002; Sullivan *et al.* 2004), changes in predator-prey relationships (Shine and Koenig 2001; Sullivan *et al.* 2004), and changes in the genetic structure of the receiving population (Dodd and Seigel 1991; Stockwell *et al.* 1996; Whiting 1997; Shine and Koenig 2001) must be addressed in LDT programs. For snakes, LDT has resulted in significant negative effects on individuals including; altered movement patterns, atypical behaviour, and increased mortality rates (Blanchard 1937; Stickel and Cope 1947; Fitch and Shirer 1971; Landreth 1973; Galligan and Dunsen 1979; Nowak 1997; Reinert and Rupert 1999; Johnson *et al.* 2000; Plummer and Mills 2000; Nowak *et al.* 2002; Butler *et al.* 2005a, 2005b). The available literature on LDT suggests translocation of adult snakes will be unsuccessful given the negative effects on translocated individuals.

SDT may be promising for rattlesnake conservation because individuals are translocated to nearby, potentially familiar habitat, thereby reducing concerns regarding habitat requirements, disease transfer, predator-prey relationships, and population genetics. Additionally, SDT may reduce individual level negative effects that have been associated with LDT because the snakes are moved near or within their normal home range. Thus, SDT has become a popular management tool to reduce rattlesnake-human conflict in wildlife agencies across North America (Nowak 1997; Hardy *et al.* 2001).

Given the popularity of SDT, but a lack of knowledge of its effects on rattlesnakes, and of its effectiveness as a management tool, I investigated rattlesnake-human conflict in British Columbia, Canada. SDT is currently the recommended management practice for the *threatened* Western Rattlesnake (MWLAP 2001). I had two main goals: 1. to determine the effects of SDT on Western Rattlesnakes; and 2. to determine the effectiveness of SDT as a management tool.

Effects of Short-distance Translocation

From a rattlesnake's perspective, SDT is successful when the risk of human-induced mortality is removed and translocated individuals are not otherwise negatively affected. Two published SDT studies on snakes examined the effects of translocation, and they reported conflicting results. The first study detected no evidence of lasting negative effects on translocated Timber Rattlesnakes (*Crotalus horridus*) (Sealy 1997), whereas the second study suggested SDT led to increased mortality rates in translocated Western Diamondbacked (*Crotalus atrox*), Black Tailed (*Crotalus molossus*), and Tiger (*Crotalus tigris*) Rattlesnakes (Hare and McNally 1997). Given these conflicting results, further study is required to elucidate the effects SDT may have on Western Rattlesnakes.

Although the movement of a rattlesnake away from an area of human activity can mitigate the immediate danger of human-induced mortality, unique aspects of rattlesnake life history suggest a potential for SDT to have negative effects. Western Rattlesnakes, like many other rattlesnake species, use specific habitats and locations within those habitats at different times of the year for hibernation, reproduction, refuge, and foraging (Macartney 1985; Nowak 1997; Hardy and Greene 1999). SDT away from these areas may disrupt normal activity patterns, thus I predicted SDT would cause rattlesnakes to move further, at a higher rate, at a higher frequency, and increase the size of their activity ranges when compared to non-translocated rattlesnakes. Movement in snakes is expensive in terms of energy use and predation risk (Gregory *et al.* 1987; Bonnet *et al.* 1999), thus snakes should normally move such that their fitness is maximized (Diller and Wallace 1996; Blouin-Demers and Weatherhead 2001). However, translocated snakes may use proportionally more energy if their activity patterns are disrupted or altered. Snakes that move more often will have less time to accumulate energy for growth, maintenance, and reproduction and may place themselves at a greater risk of mortality and predation. Therefore, I predicted that translocated rattlesnakes would have a lower body condition, decreased mating success, and increased mortality rates compared to non-translocated rattlesnakes.

Short-distance Translocation as a Management Tool

If SDT is successful from a management perspective, the risk of rattlesnake-human interaction must be removed so that the snake does not return to its original location during the same active season as the translocation event. Three previously published studies examined the performance of SDT as a management strategy for

rattlesnakes and reported inconsistent results. Hardy *et al.* (2001), using mark and recapture methods, performed SDT on 46 Black Tailed (*Crotalus molossus*) and 8 Western Diamondbacked (*Crotalus atrox*) Rattlesnakes, and concluded SDT was not successful because recapture rates in areas of human activity were 33% and 56% over two consecutive years of study. In a mark and recapture study by Sealy (1997), SDT was considered a successful management strategy for 31 Timber Rattlesnakes (*Crotalus horridus*). Only 4% of relocated individuals were recaptured in an area of human activity within the same year, and rattlesnakes displayed active avoidance of these areas. Hare and McNally (1997), using mark and recapture methods, performed SDT on 97 Western Diamondbacked (*Crotalus atrox*), Black Tailed (*Crotalus molossus*) and Tiger (*Crotalus tigris*) Rattlesnakes with a 2% recapture rate. However, it is likely the recapture rates in the above studies were underestimated because the authors used biased methods to determine their recaptures rates. When using mark and recapture methods, snakes may have returned to conflict areas but remained undetected.

SDT may be unsuccessful as a management tool because Western Rattlesnakes display homing behaviour to specific habitats and locations within those habitats to fulfill their life history requirements (Macartney 1985; Nowak 1997; Hardy and Greene 1999). Therefore, I predicted SDT of rattlesnakes would be characterized by high rates of return to areas of human activity. Furthermore, I predicted translocated rattlesnakes would display site fidelity by homing to the same locations that were occupied prior to SDT.

MATERIALS AND METHODS

Study Methods

a. Study Site

The study site was located in the southern Okanagan valley, on the Osoyoos Indian Reserve, which is situated on the east side of the town of Osoyoos, British Columbia, Canada (119.4°W and 49.28°N; inset Figure 1). I conducted this study on a 470ha site located at the south end of the Osoyoos Indian Reserve. The site was bordered by Osoyoos to the south, Lake Osoyoos to the west, and steep, rocky cliffs to the east. On the valley floor, the habitat consisted of a shrub-steppe dominated by antelope brush (*Purshia tridentate*) and big sagebrush (*Artemisia tridentate*). The margins of the valley consisted of steep rocky cliffs containing a mix of talus and rock outcrops with ponderosa pine (*Pinus ponderosa*) stands dispersed throughout. The study area lay within the bunchgrass and ponderosa pine biogeoclimatic zones of British Columbia (Lloyd *et al.* 1990). At the south end of the study site, the main anthropogenic developments included: a campground (a), along the shore of Lake Osoyoos, a winery (b), a condominium resort (c), a golf course (d), and the associated roads which draw thousands of visitors annually (Figure 1).

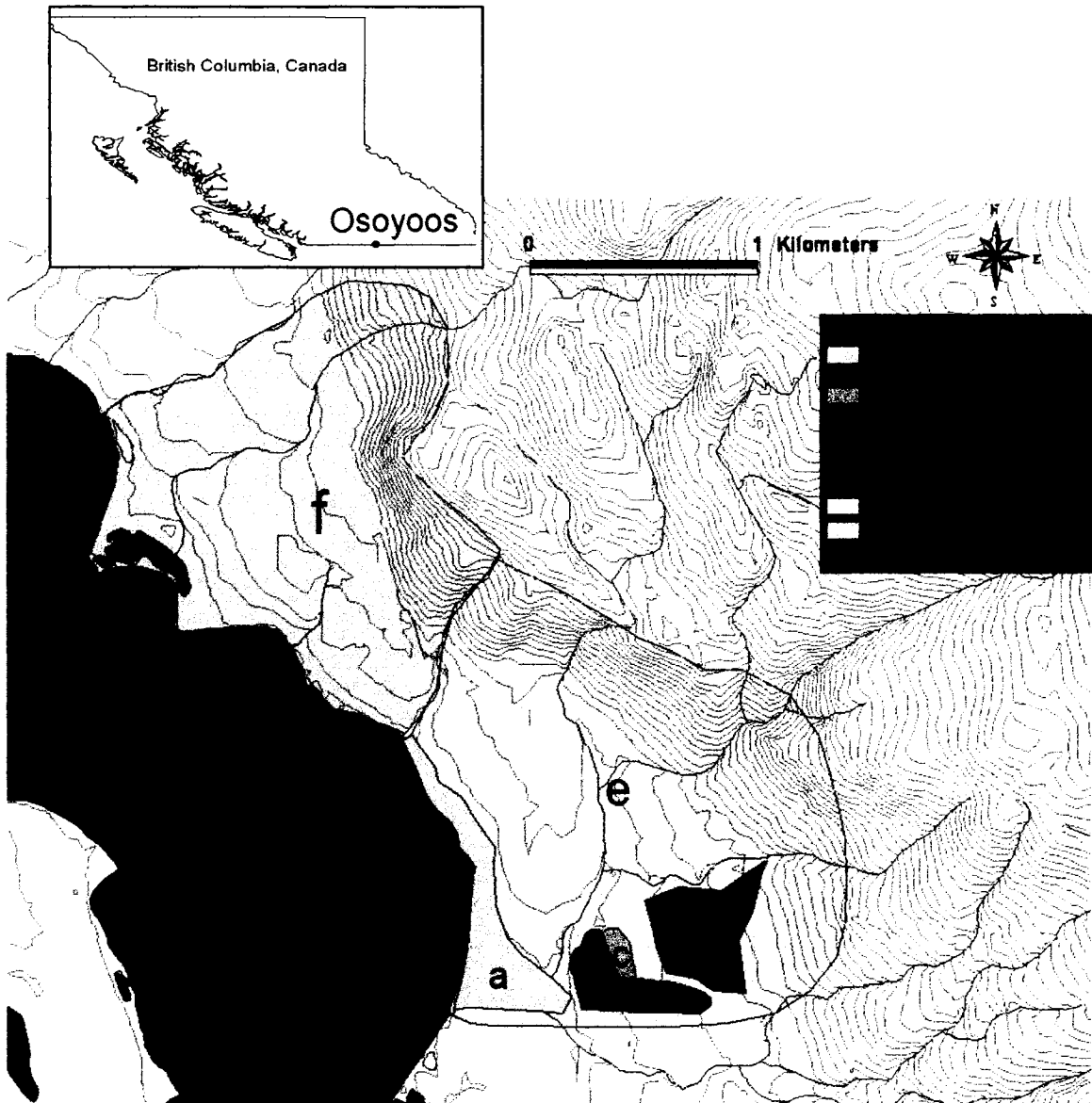


Figure 1: Map of the study site, and its location in British Columbia, including the locations and types of anthropogenic developments, and experimental translocation and control treatments.

b. Radio-Telemetry

Radio-Transmitter Implantation

Western Rattlesnakes were located by direct search effort on foot and by incidental encounters by visitors and staff. All rattlesnakes encountered were captured and returned to the lab, where they were weighed, measured, sexed, and marked before release. A total of 31 adult male rattlesnakes were surgically implanted with radio-transmitters (Holohil Systems Inc., model SB-2T). The transmitters had a battery life of 12 months and weighed 5g. To minimize effects on individuals, transmitters never weighed more than 3.5% (mean 2.3%) of total body mass. I elected to implant only adult male rattlesnakes with radio-transmitters to increase statistical power associated with a small radio-telemetry sample size. Surgical implantations did not occur after August 1st to ensure adequate time for healing before onset of the hibernation period (Rudolph *et al.* 1998).

All surgical procedures followed the methods of Reinert and Cundall (1982) with modifications by Reinert (1992) and Willson (2005). Surgical candidates were anesthetized at a veterinary hospital in an induction chamber using sevoflurane. Antibiotics (enrofloxacin) and analgesics (meloxicam) were administered before and after all surgical procedures. After a 24-48 h recovery period, transmitter-equipped rattlesnakes were released at their initial capture locations before the onset of the translocation experiment. At the end of the 'battery life', transmitters were removed following the procedures described above. All surgical and handling procedures were conducted with approval from the following permits: Environment Canada Species at

Risk Act permit number 59-05-0353; British Columbia Wildlife Act permit number PE06-21403; and University of Guelph Animal Utilization Protocol 05R037.

Radio-Tracking

After release from surgery, all snakes equipped with radio-transmitters were located approximately every 2 days until they entered hibernation in the fall. Snakes were located using a 3-element yagi antenna and a portable radio-telemetry receiver (AVM Instrument Co., LA12-Q; Communications Specialists Inc., R-1000). At each location, a handheld geographical positioning system (GPS) unit (Garmin Ltd., GPS Map 76s) was used to record the geographic location of the snake in Universal Transverse Mercators (UTMs). At each telemetry location, I recorded the following data: date, time, description of location, GPS coordinates with estimated accuracy, habitat occupied, behaviour, disturbance caused by researcher, and distance from last location. Each transmittered rattlesnake was recaptured, weighed, and the snout-vent length (SVL) was measured just before hibernation in the fall to assess their general condition in 2004. In 2005, I recaptured, weighed, and measured the SVL of all rattlesnakes equipped with a transmitter once per month between May and October to monitor condition.

c. Experimental Translocation

To conduct the short-distance translocation experiment, the study site was partitioned into two separate sites, each containing one treatment. The translocation treatment was applied to the south end of the study site (e in Figure 1) to encompass all human developments (i.e. campground, winery, condominium resort, golf course, and associated roads). The north half of the study site (f in Figure 1) was free of human development, and was used as a control.

As soon as a snake in the translocation treatment was detected in an area of human activity, it was relocated to habitat free of human development on the study site. The direction of relocation was selected at random from a restricted set of compass bearings, which included only directions that would result in a translocation to natural habitat, rather than to adjacent human modified habitat. All translocations were moved at a distance of 500m from the capture location. I used a GPS unit with a built-in compass (Garmin Ltd., GPS MAP 76S) to measure the translocation distance and find the compass bearing. Based on dispersal patterns of the Western Rattlesnake in British Columbia, a distance of 500m was considered a 'short translocation' (Macartney 1985; Macartney *et al.* 1988; Bertram *et al.* 2002). This distance placed rattlesnakes in potentially familiar habitat which was near or within their normal home-range, and permitted rattlesnakes to return to their initial capture location.

Rattlesnakes were only translocated after they entered an area of human activity. As a result, there were a variable number of translocations per individual rattlesnake. In addition, rattlesnakes monitored over two full active seasons were translocated a different number of times between each year. Given this variation in the number of translocations between years and individuals, I considered translocated snakes ($n = 5$) monitored over two active seasons as two independent samples, which might result in some pseudoreplication. If a snake on the translocation site did not enter an area of human activity during the active season, it was considered in the control group for analysis.

Non-translocated (i.e. control) snakes were subdivided into 3 treatments to control for possible effects related to the stress of capture and transportation. The 3 treatments comprised 3 levels of handling; no handling, low handling (i.e. handled once over the

entire active season), and high handling (i.e. handled five times over the entire active season). Handling consisted of capturing a rattlesnake and transporting it 500m before releasing it back at its exact capture location. All rattlesnakes given a handling control or translocation treatment were transported on foot in a pillowcase.

Statistical Methods

a. Data Analyses

Only rattlesnakes that were tracked for a full active season were included in the analyses to avoid bias from incomplete data sets. Because the Western Rattlesnake displays strong fidelity to a specific hibernaculum (Macartney 1985), I added the hibernaculum location as an initial telemetry data point for individuals that were captured away from their hibernation site in the spring. I excluded multiple telemetry data points from each individual at the onset and conclusion of the hibernation period to avoid bias in spatial statistics. Egress from hibernation in the spring was represented by a single telemetry data point, and ingress in the fall was represented by two consecutive telemetry data points at an individual's hibernaculum.

All spatial data were mapped and analyzed in ArcView GIS version 3.2a (Environmental Systems Research Institute, 1999). Calculation of movement and spatial statistics was completed using the Animal Movement extension version 2.0. beta (Hooge and Eichenlaub 2000).

b. Statistical Analyses

All data were analyzed using the statistical computer program SPSS version 12.0 (SPSS Inc. 2003). Levene's test of homogeneity of variance was used to verify that variances between groups were homogeneous (Neter *et al.* 1990). Data were tested for

normality by visual examination of histograms and the Kolmogorov-Smirnov goodness of fit test (Zar 1999). For all parametric tests, non-homogenous and non-normally distributed data were transformed to meet assumptions. All means are reported \pm one standard deviation unless otherwise stated. Statistical significance was determined using a p-value of ≤ 0.05 .

c. Movement Patterns

All movement pattern variables represent minimum rather than exact values for two reasons. First, snakes were tracked once every 48h, so it is likely some movements went undetected. Second, consecutive telemetry data points were connected with a straight line, and it is unlikely that snakes travel in straight line when moving (Secor 1994; Beck 1995; Webb and Shine 1997). Consecutive telemetry data points less than 10m apart were excluded from the analyses to account for GPS error. Thus, each telemetry point greater than 10m apart was considered a unique location. For snakes in the translocation treatment, 500m translocation distances were subtracted from the movement pattern analyses. The following indices of movement were compared between treatments to determine if translocation had an impact on rattlesnake movement patterns.

Total Distance Moved – the sum of linear distances between consecutive telemetry data points. The total distance moved (TDM) represents the movement capacity of an individual rattlesnake over a given time period.

Rate of Movement – the sum of the distance between successive telemetry data points, divided by the total number of movements. The rate of movement, expressed in mean distance per movement (MDM), is a measure of movement only when movement occurs.

Frequency of Movement – the sum of the number of unique locations divided by the total number of days monitored in the appropriate time frame. Frequency of movement, expressed in the number of movements per day (NMD) is a measure of the activity level in snakes (Webb and Shine 1997).

Full Season Movement Pattern Analyses

I examined the effects of handling control treatment (none, low, and high), and SDT treatment (translocation and control) on the total distance moved and the frequency of movement using ANCOVA with the number of days monitored as a covariate because rattlesnakes included in the analyses were monitored over a variable number of days. Additionally, I analyzed the rate of movement with the total number of movements as a covariate because there was variation in the number of movements between individuals.

The number of translocations per individual varied because snakes were translocated only when they entered an area of human activity. This variation allowed me to examine the cumulative effects of translocation (i.e. number of translocations per individual) on all movement variables described above using linear regression.

Seasonal Movement Pattern Analyses

Adult male rattlesnakes have a discrete mating season characterized by active searching for females (Reinert and Zappalorti 1988; Secor 1994; Duvall and Schuett 1997). I quantified the onset and conclusion of the mating season to define three biologically relevant sub-seasons in which to analyze movement patterns. The period preceding the mating season was called dispersal because rattlesnakes moved from hibernacula to summer activity areas. The period following the mating season was called ingress because rattlesnakes moved from their summer activity areas to their hibernacula.

The mean mating season duration over 2004 and 2005 was 42 days, which was quantified using the time between first and last observed mating events. For this analysis, I applied a mating season duration of 42 days to each year separately starting with the first observed mating event. In 2004, the mating season was from July 20 to Aug 31, and in 2005 the mating season was from July 9 to Aug 20.

I analyzed measures of movement patterns by treatment and season using repeated measures MANOVA. Post-hoc univariate ANOVA and matched paired t-test were then used to identify significant differences. The cumulative effects of translocation, measured in number of translocations per individual, on movement patterns were analyzed by season using linear regression where sample size permitted.

d. Activity Range Analyses

The following variables were compared between translocation and control treatments to determine if SDT had an impact on how Western Rattlesnakes utilized their spatial environment over a full active season.

Range Length (RL) – the maximum straight line distance between any two telemetry data points, a measure of the maximum linear dispersal in the environment.

Ratio of Range Width to Range Length (RW:RL) – a measure of the shape of the activity range. Values closer to 1 indicate a square activity range shape and values closer to 0 indicate a linear activity range shape.

Minimum Convex Polygon (MCP) – a measure of the total area utilized over a given time period. The MCP is likely to contain large areas of space that are not utilized in normal movements by an individual (White and Garrott 1990). The MCP provides a rough comparison of space use between translocation and control treatments.

I tested for differences in RL within the control treatment (level of handling control), and between treatments using ANCOVA with the number of days monitored as a covariate because snakes were monitored for a variable number of days. Because RW:RL is a ratio variable, it was tested within the control treatment and between treatments using ANCOVA with RL as a covariate. The size of the MCP activity range is sensitive to the number of telemetry points used in the analysis (White and Garrott 1990; Reinert 1992), so MCP area was tested within the control treatment and between treatments using ANCOVA with the number of telemetry points as a covariate. Linear regression was used to test for possible cumulative effects of translocation, measured in the number of translocations per individual, on activity range variables.

e. Condition Analyses

To assess the size-independent condition of rattlesnakes at a given point in time, the residuals of the linear regression of mass to snout-vent length (SVL) for each treatment group were calculated (Green 2001; Shine *et al.* 2001). For all individuals monitored in 2005, condition values were calculated at three points in time, each corresponding to a specific season. To determine if there was a difference in condition, I analyzed the residuals within-group (by season) and between group (treatment) using MANOVA with repeated measures.

f. Behaviour Analyses

The effects of translocation on rattlesnake behaviour were determined by comparing mating success, frequency of exposure, and habitat use between treatments. Mating success was defined as the number of mating events where copulation was observed. The number of successful mating events was considered a minimum number of

mates per individual because some mating events may have gone undetected with a 48h tracking interval. A t-test was used to determine if there was a difference in mating success between treatments. At each telemetry data point, rattlesnakes were classified as concealed, when 25% or less of their body was visible; basking, when 26 to 100% of the body was visible; or moving. These proportions sum to one, thus they are not independent (Aebischer et al. 1993). To solve this issue, I log-ratio transformed each proportion using the percent of telemetry locations moving as the denominator, following the methods of Aitchison (1986). I tested for differences in the frequency of exposure between treatments using MANOVA on the transformed data. Relative differences in habitat use over the full active season were determined by comparing the percent of telemetry data points in the five major habitat types on the study site which included: shrub-steppe, ponderosa pine stand, riparian, rock-outcrop, and wetland. The relative habitat use data also suffers from non-independence because it is proportional data. Following the methods described above, I log-ratio transformed habitat data with the percent of telemetry locations in rock-outcrop as the denominator. I tested for a difference in habitat use between treatments using MANOVA on the transformed data.

g. Multiple Translocation Analyses

For all rattlesnakes that required more than a single translocation, linear regression was used to determine the relationship between the number of translocations per individual, and the mean distance traveled and mean time to return to an area of human activity over the full active season to determine if multiple translocations affected the success rate of SDT. The data were also examined for seasonal trends in the mean time and distance to return to an area of human activity.

To determine if rattlesnakes selected or avoided specific locations in areas of human activity after unsuccessful SDTs, the distances between successive capture locations were measured. A chi-square analysis tested if the distribution of these distances was different from a null distribution (Zar 1999). The null distribution represents a situation where no selection occurred because the individual did not preferentially return to or avoid a specific location in an area of human activity. Post-hoc subdivision of the chi-square analysis was used to identify significant differences (Zar 1999).

RESULTS

From April 1, 2004 to October 15, 2005, a total of 363 individual Western Rattlesnakes (*Crotalus oreganus oreganus*) was captured on the study site. From these captures, 31 individuals were implanted with radio-transmitters. All radio-tracked rattlesnakes were adult males that ranged between 63cm to 80cm in snout-vent length. Full season data were obtained from 23 rattlesnakes, representing 28 full active seasons (n= 18 tracked over a single active season and n= 5 tracked over two full active seasons). Five rattlesnakes monitored on the translocation site (Figure 1) were considered a part of the control treatment because they did not enter an area of human activity, and were not translocated. The translocation and control treatments were each represented by data from 14 full active seasons. Rattlesnakes in the control treatment were monitored for an average of 141.6 ± 18.9 days and located on average every 2.4 ± 0.2 days (Appendix A). From the control treatment, 5 individuals were assigned to the no handling group, 5 individuals to the low handling group and 4 individuals to the high handling group. Rattlesnakes in the translocation treatment were monitored for an average of 153.2 ± 19.3 days and located on average every 2.3 ± 0.2 days (Appendix A). On average, each individual in the translocation treatment was translocated 3.4 (range 1-7) times.

Effects of Short-distance Translocation

a. Full Season Movement Patterns

Total Distance Moved

No significant difference in the total distance moved (TDM) was detected among the three levels of handling control ($F_{2,10} = 0.480$, $P = 0.632$), so they were pooled for comparison to the translocation treatment. The mean TDM was $5838 \pm 1271\text{m}$ for the control treatment and $7188 \pm 1369\text{m}$ for the translocation treatment ($F_{1,25} = 6.337$, $P = 0.019$) (Table 1). There was no evidence of an interaction between the number of days monitored and treatment on the TDM ($F_{1,24} = 0.255$, $P = 0.618$). There was a significant positive relationship between the number of translocations per individual and the TDM over the full active season ($F_{1,11} = 9.338$, $P = 0.010$, $R^2 = 0.438$) (Figure 2).

Rate of Movement

The movement rate was not significantly different among the three levels of handling control ($F_{2,10} = 0.399$, $P = 0.681$), so they were pooled for comparison to the translocation treatment. Rattlesnakes in the control treatment moved on average $142 \pm 37\text{m}$ per movement and rattlesnakes in the translocation treatment moved on average $160 \pm 33\text{m}$ per movement ($F_{1,25} = 6.056$, $P = 0.021$) (Table 1). There was no evidence of an interaction effect between the number of movements per individual and treatment on the movement rate ($F_{1,24} = 0.657$, $P = 0.426$). The regression of the movement rate on the number of translocations per individual was positive but not significant ($F_{1,12} = 3.594$, $P = 0.082$, $R^2 = 0.230$).

Table 1: Mean full season movement pattern values, with standard deviations, for Western Rattlesnakes in control and translocation treatments. Letters indicate a significant difference between treatments at $\alpha = 0.05$ by column.

	Total distance moved (m)	Rate of movement (m/movement)	Frequency of movement (# of movements/day)
Control (n=14)	5838 \pm 1271 ^a	142 \pm 37 ^a	0.29 \pm 0.04
Translocation (n= 14)	7188 \pm 1369 ^b	160 \pm 33 ^b	0.30 \pm 0.05

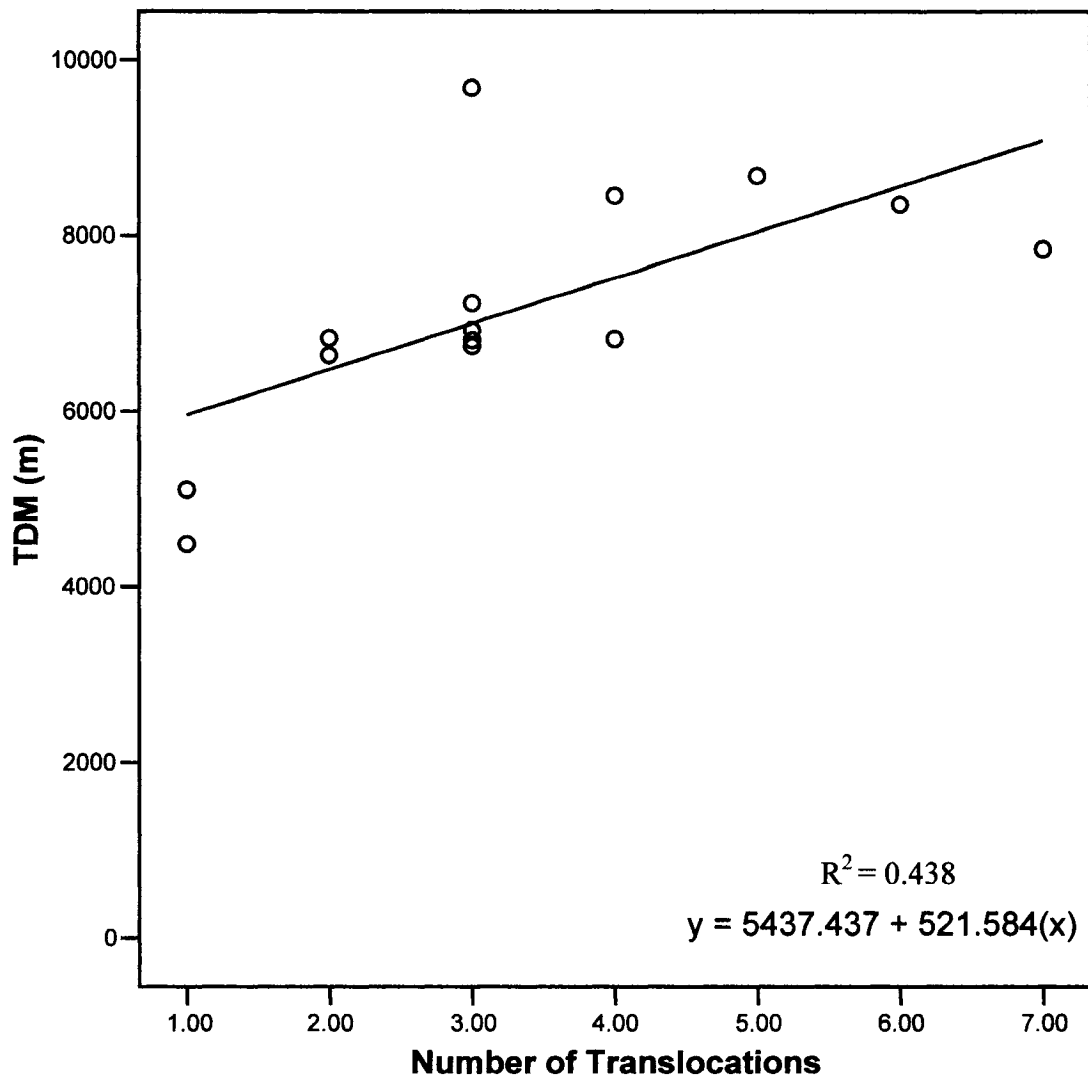


Figure 2: Linear regression of the total distance moved (TDM), in meters, over the full active season on the number of translocations per individual.

Frequency of Movement

The frequency of movement, measured in number of movements per day (NMD), was not significantly different among the 3 levels of handling control ($F_{2,10} = 0.386$, $P = 0.690$), so they were pooled for comparison to the translocation treatment. The mean frequency of movement was 0.29 ± 0.04 and 0.30 ± 0.05 movements per day for the control and translocation treatments respectively ($F_{1,25} = 1.662$, $P = 0.209$) (Table 1). There was no significant interaction between the number of days monitored and treatment on the frequency of movement ($F_{1,24} = 0.721$, $P = 0.404$). There was no significant relationship between the number of translocations per individual and the frequency of movement ($F_{1,12} = 0.192$, $P = 0.669$, $R^2 = 0.016$).

b. Seasonal Movement Patterns

Total Distance Moved

A significant interaction effect between treatment and season on TDM was found using repeated measures MANOVA examining the effect of treatment on TDM by season ($F_{2,25} = 6.739$, $P = 0.005$). Post-hoc tests revealed rattlesnakes in the translocation treatment moved significantly further than rattlesnakes in the control treatment during the dispersal season ($F_{1,26} = 18.856$, $P < 0.001$), but not during the mating ($F_{1,26} < 0.000$, $P = 0.985$), or ingress seasons ($F_{1,26} = 0.018$, $P = 0.896$). Within the control treatment, there was no significant difference in TDM between the dispersal and mating seasons ($t_{13} = -1.806$, $P = 0.094$), but rattlesnakes in the control treatment had a significantly higher TDM in the mating ($t_{13} = 5.552$, $P < 0.001$) and dispersal ($t_{13} = 4.576$, $P = 0.001$) seasons, when compared to the ingress season. Within the translocation treatment, rattlesnakes moved significantly further during the dispersal season when compared to the mating season

($t_{13} = 2.524$, $P = 0.025$). The TDM values during both the mating ($t_{13} = 5.423$, $P < 0.001$) and dispersal seasons ($t_{13} = 6.045$, $P < 0.001$) were significantly higher than the ingress season (Figure 3). There was a strong positive significant relationship between the number of translocations per individual and TDM over the dispersal season ($F_{1,11} = 24.855$, $P < 0.001$, $R^2 = 0.693$) (Figure 4). There was insufficient sample size to test for cumulative effects of translocation during the mating season for all movement variables. No translocation events occurred during the ingress season, and linear regression was not performed on any movement variables for this season.

Rate of Movement

A repeated measures MANOVA, found no significant interaction between treatment and season ($F_{2, 25} = 0.930$, $P = 0.408$), but a main effect of season on the movement rate was significant ($F_{2,25} = 11.060$, $P < 0.001$). For control snakes, the movement rate was significantly higher during the mating season compared to the dispersal ($t_{13} = -3.613$, $P = 0.003$) and ingress ($t_{13} = -3.682$, $P = 0.003$) seasons. No difference in movement rate was detected between dispersal and ingress ($t_{13} = 1.217$, $P = 0.245$). No significant difference was detected in movement rate between seasons within the translocation treatment (Figure 5). There was a significant relationship between the number of translocations per individual and the movement rate in the dispersal season ($F_{1,11} = 10.617$, $P = 0.008$, $R^2 = 0.491$) (Figure 6).

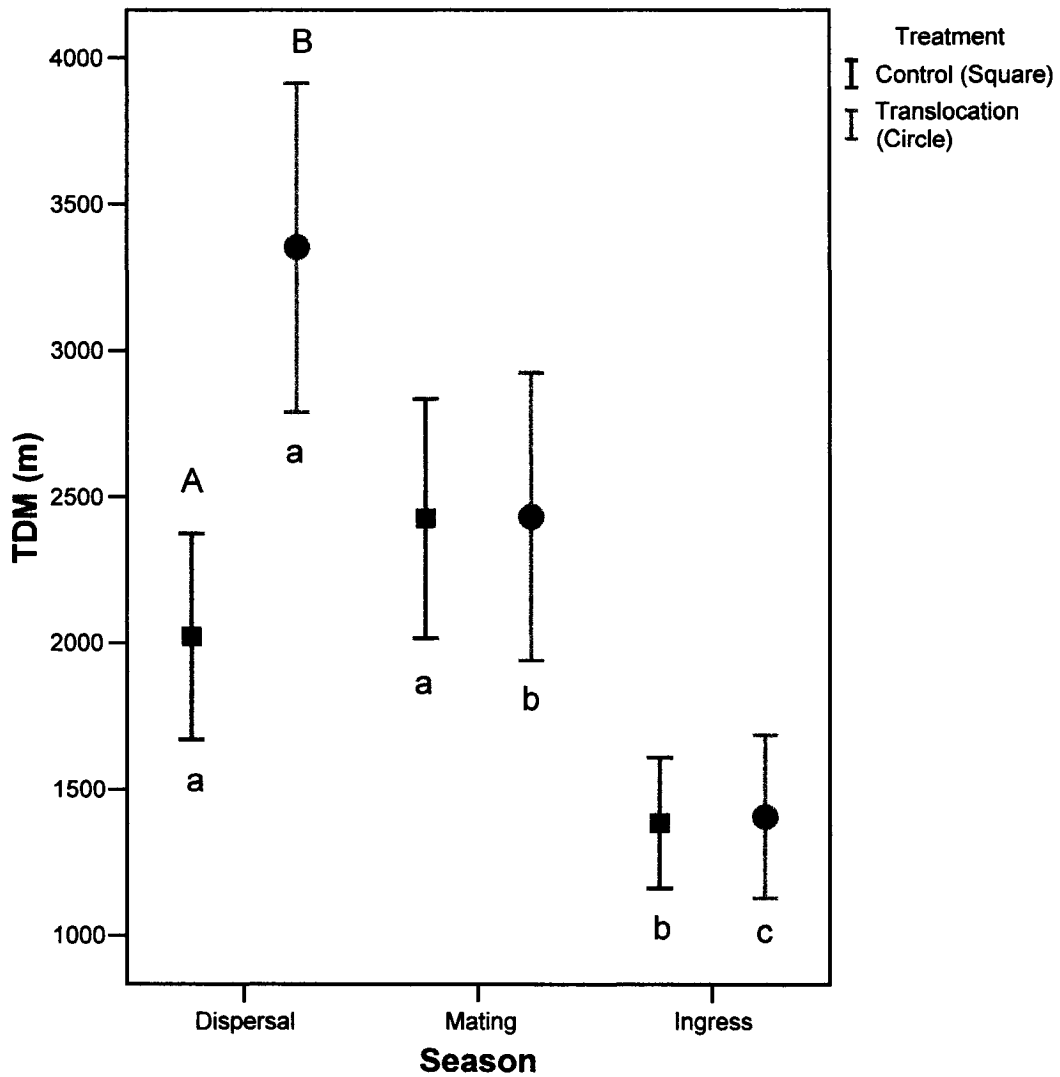


Figure 3: Comparison of the mean total distance moved (TDM), in meters, with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments by season. Uppercase letters (above bars) indicate a significant difference between treatments within a season and lowercase letters (below bars) indicate a significant difference between seasons within a treatment at $\alpha = 0.05$.

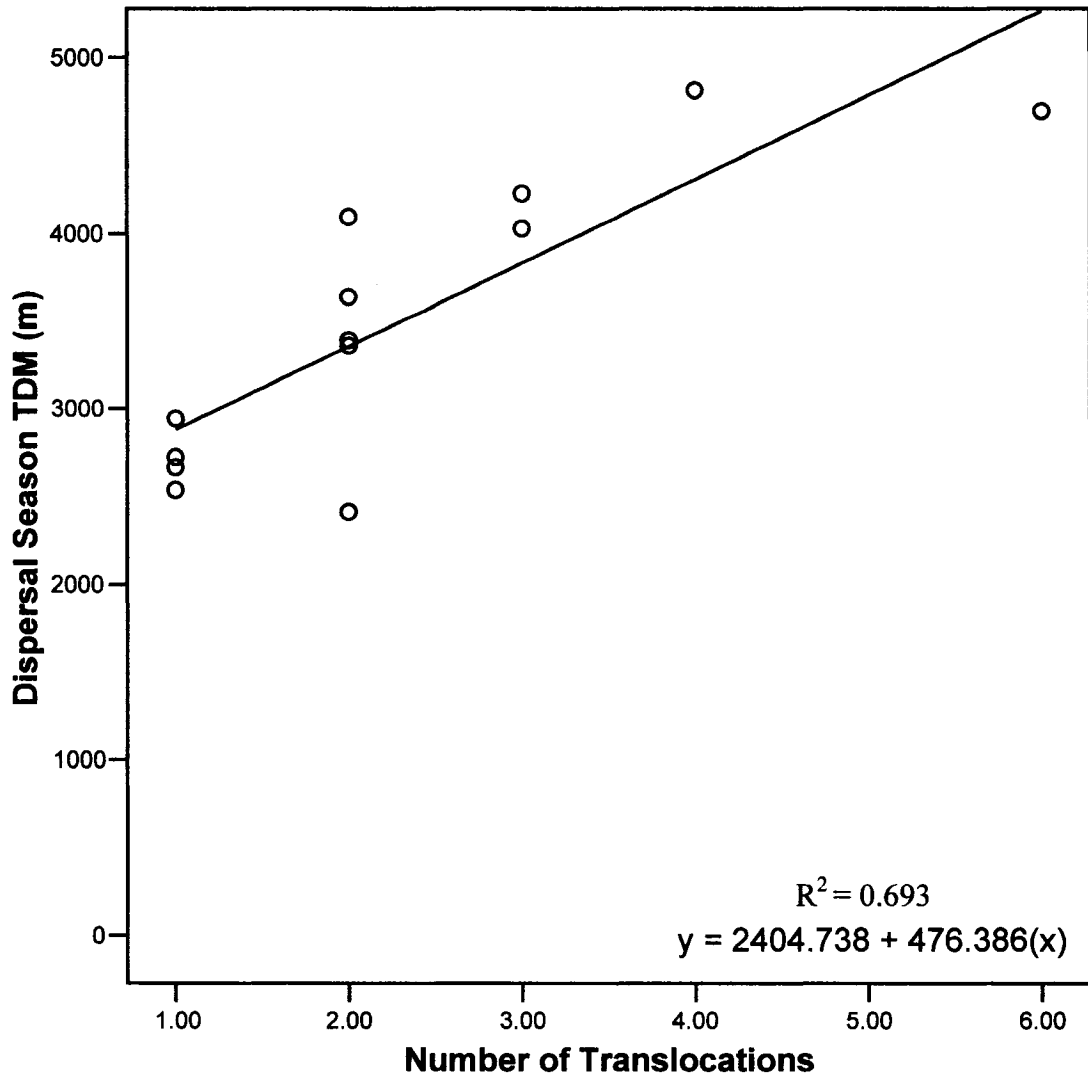


Figure 4: Linear Regression of the total distance moved (TDM), in meters, on the number of translocations per individual during the dispersal season.

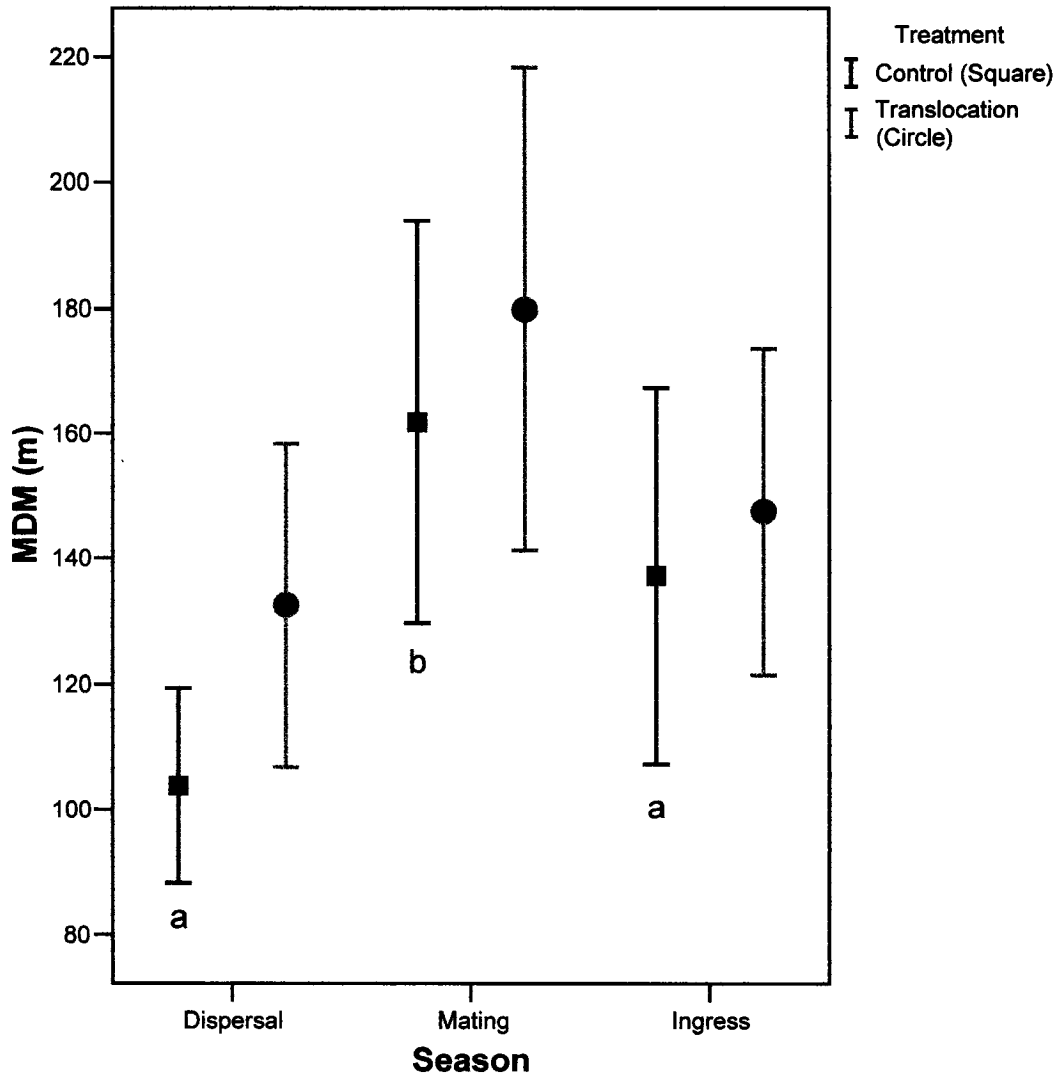


Figure 5: Comparison of the movement rate, measured in mean distance per movement (MDM), with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments by season. Letters indicate a significant difference between seasons within a treatment at $\alpha = 0.05$.

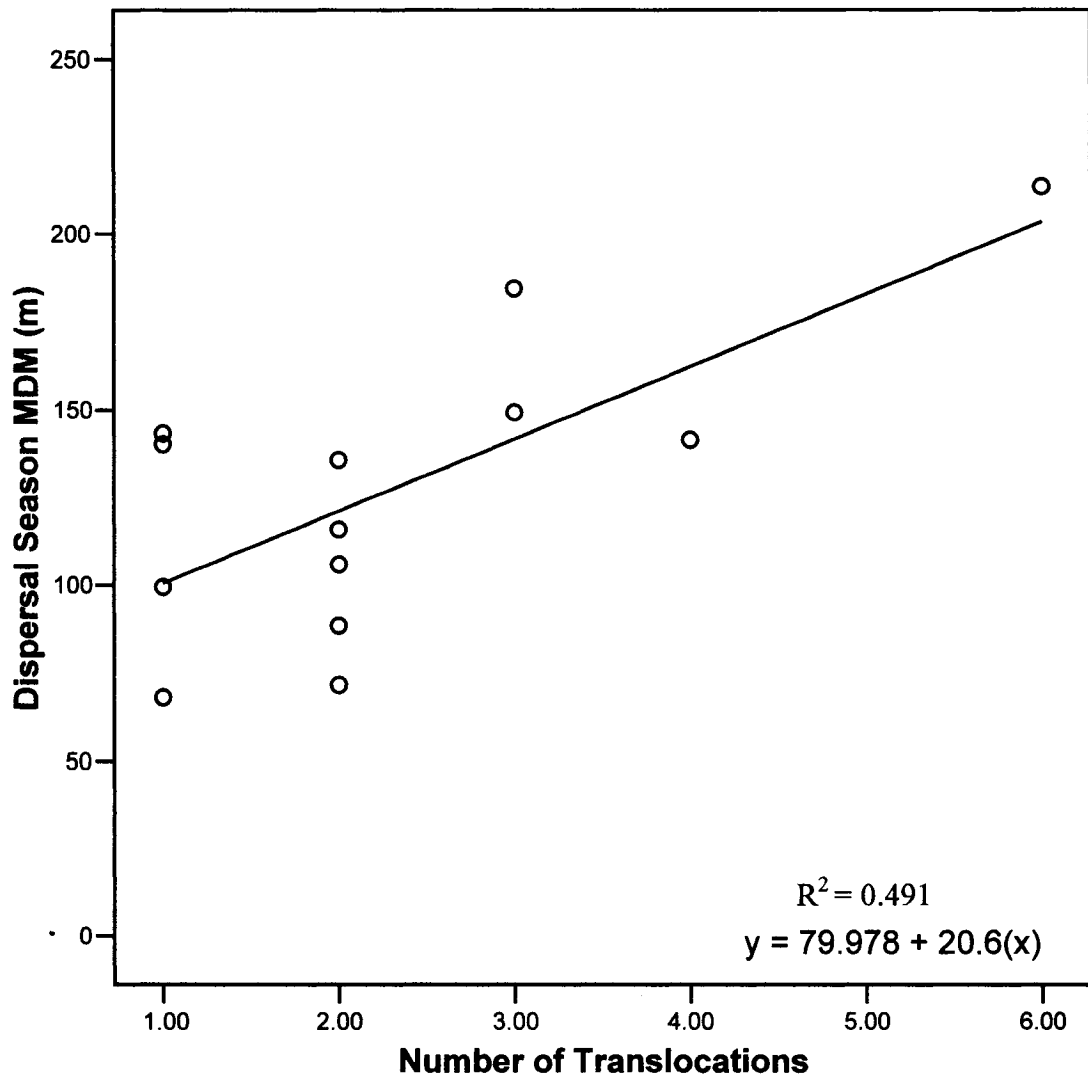


Figure 6: Linear regression of the movement rate, measured in mean distance per movement (MDM), on the number of translocations per individual in the dispersal season.

Frequency of Movement

A repeated measures MANOVA, found no significant interaction between treatment and season ($F_{2,25} = 2.483$, $P = 0.104$), but a main effect of season on the movement frequency was significant ($F_{2,25} = 14.751$, $P < 0.001$). Within the control treatment, rattlesnakes moved more frequently during the mating season when compared to the dispersal ($t_{13} = -4.710$, $P < 0.001$), and ingress ($t_{13} = 5.219$, $P < 0.001$) seasons, and there was no significant difference in movement frequency between dispersal and ingress ($t_{13} = 1.384$, $P = 0.190$). Within the translocation treatment, the movement frequency during dispersal was not significantly different from the mating season ($t_{13} = -0.202$, $P = 0.843$), but it was higher in both the dispersal ($t_{13} = 2.190$, $P = 0.047$) and mating ($t_{13} = 2.722$, $P = 0.017$) seasons, when compared to the ingress season (Figure 7). During the dispersal season, there was no significant relationship between the number of translocations per individual and the movement frequency ($F_{1,11} = 0.066$, $P = 0.802$, $R^2 = 0.006$).

c. Activity Range

Range Length

The range length (RL), was not significantly different among the 3 levels of handling control ($F_{2,11} = 0.019$, $P = 0.981$), so they were pooled for comparison to the translocation treatment. Mean RL was $1082 \pm 328\text{m}$ and $1245 \pm 285\text{m}$ for the control and translocation treatments respectively ($F_{1,25} = 3.216$, $P = 0.085$) (Table 2).

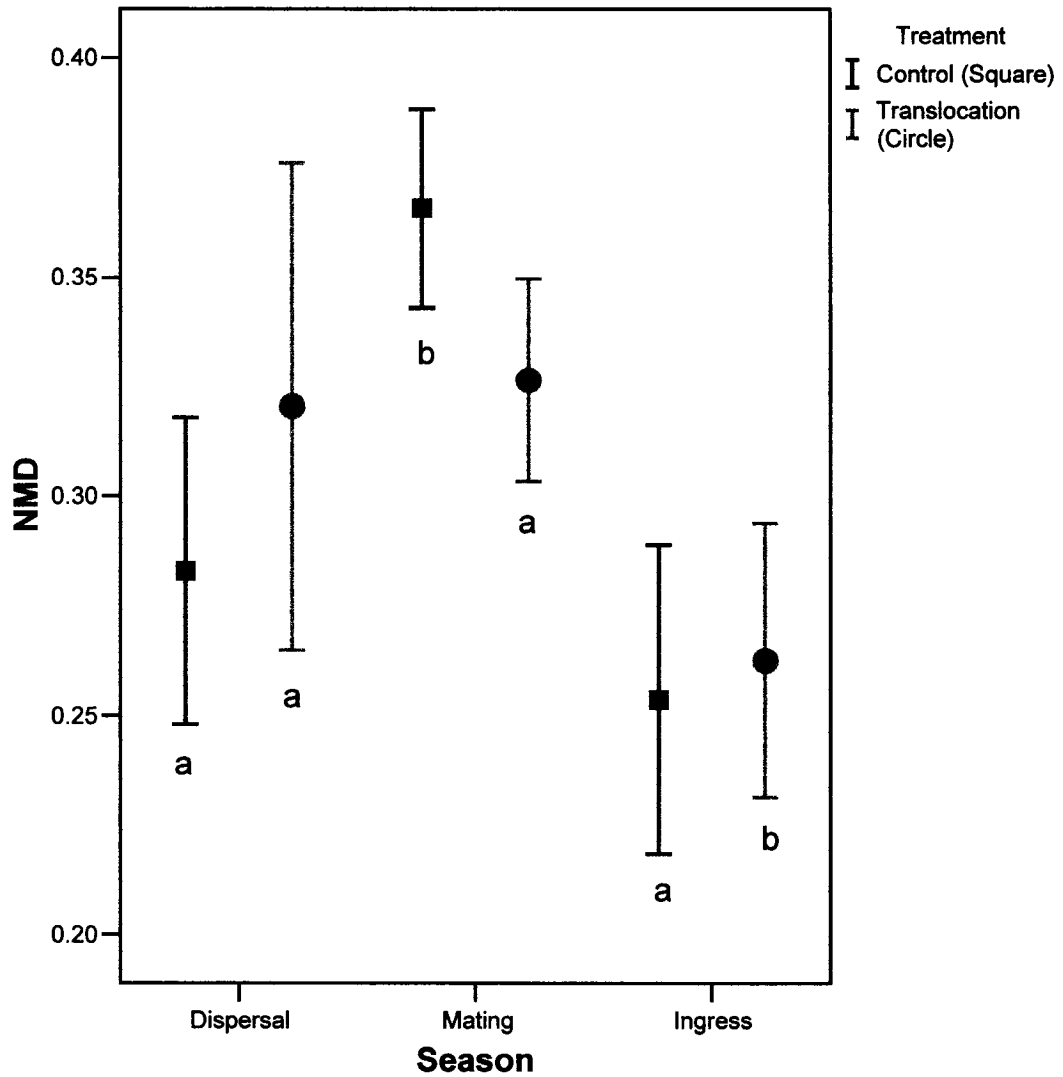


Figure 7: Comparison of the mean number of movements per day (NMD), with 95% confidence intervals, for Western Rattlesnakes in the control and translocation treatments by season. Letters indicate a significant difference between seasons within a treatment at $\alpha = 0.05$.

Table 2: Mean full season activity range values, with standard deviations, for Western Rattlesnakes in control and translocation treatments.

	Range Length (m)	Range Width: Range Length	MCP area (ha)
Control (n=14)	1082 ± 328	0.33 ± 0.15	25.1 ± 16.8
Translocation (n= 14)	1245 ± 285	0.39 ± 0.15	37.4 ± 10.5

There was no interaction between the number of days monitored and treatment on RL ($F_{1,24} = 0.018$, $P = 0.895$). There was no significant relationship between the number of translocations per individual and RL ($F_{1,12} = 0.062$, $P = 0.808$, $R^2 = 0.005$).

Range Width: Range Length

The ratio of range width to range length (RW:RL), was not significantly different among the 3 levels of handling control ($F_{2,11} = 0.029$, $P = 0.971$), so they were pooled for comparison to the translocation treatment. The mean RW:RL ratio for the control treatment was 0.33 ± 0.15 and 0.39 ± 0.15 for the translocation treatment ($F_{1,25} = 3.984$, $P = 0.060$) (Table 2). There was no evidence of an interaction between the range length and treatment on the RW:RL ratio ($F_{1,24} = 0.796$, $P = 0.381$). The relationship between the number of translocations per individual and the RW:RL ratio was not significant ($F_{1,12} = 2.598$, $P = 0.133$, $R^2 = 0.178$).

Minimum Convex Polygon

The area of the minimum convex polygon (MCP) was not significantly different among the 3 levels of handling control ($F_{2,11} = 0.164$, $P = 0.851$), so they were pooled for comparison to the translocation treatment. The mean MCP area for the control group was 25.1 ± 16.8 ha, and the mean MCP area for the translocation group was 37.4 ± 10.5 ha ($F_{1,25} = 3.524$, $P = 0.083$) (Table 2). No evidence of an interaction between the number of telemetry points and treatment on minimum convex polygon (MCP) size was present ($F_{1,24} = 0.159$, $P = 0.693$). There was no significant relationship between the number of translocations per individual and the MCP area ($F_{1,12} = 2.346$, $P = 0.152$, $R^2 = 0.164$).

d. Condition

There was a strong positive relationship between mass and snout-vent length (SVL) in this population of Western Rattlesnakes ($F_{1,221} = 2689.777$, $P = <0.001$, $R^2 = 0.924$) (Figure 8). Thus, the residuals of the mass to SVL regression were used as a size independent body condition index for the treatment groups. A repeated measures MANOVA found no effects of treatment ($F_{1,13} = 0.632$, $P = 0.441$) or season ($F_{2,12} = 1.852$, $P = 0.199$) on condition (Figure 9).

e. Behaviour

Mating Success

The number of mates per individual rattlesnake was compared between control and translocation treatments using a t-test. Rattlesnakes in the control treatment had on average 0.9 ± 1.0 successful mating events, and rattlesnakes in the translocation treatment had on average 1.2 ± 0.8 successful mating events ($t_{13} = -0.835$, $P = 0.411$).

Frequency of Exposure

The effect of treatment on the log-ratio transformed frequency of exposure was not significant ($F_{2,25} = 1.329$, $P = 0.283$). Rattlesnakes in the control treatment were found concealed on $42.6 \pm 9.8\%$ of telemetry locations, basking on $48.6 \pm 9.8\%$ of telemetry locations, and moving on $8.7 \pm 3.4\%$ of telemetry locations. In the translocation treatment, rattlesnakes were found concealed on $47.5 \pm 7.3\%$ of telemetry locations, basking on $42.8 \pm 8.2\%$ of telemetry locations, and moving on $9.5 \pm 4.0\%$ of telemetry locations (Figure 10).

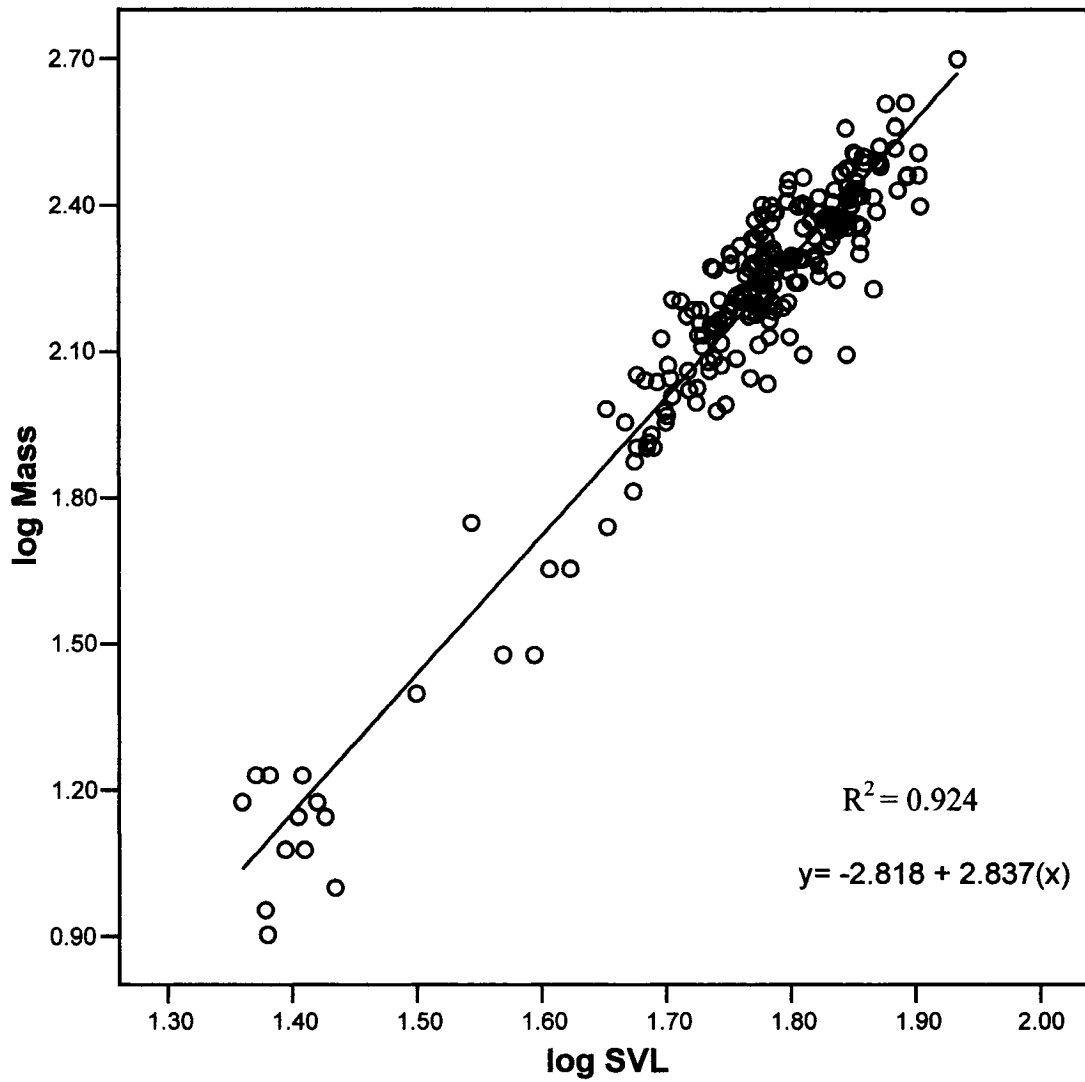


Figure 8: Log-log linear regression of mass on snout-vent length of 222 individual Western Rattlesnakes captured between April 2004 and October 2005.

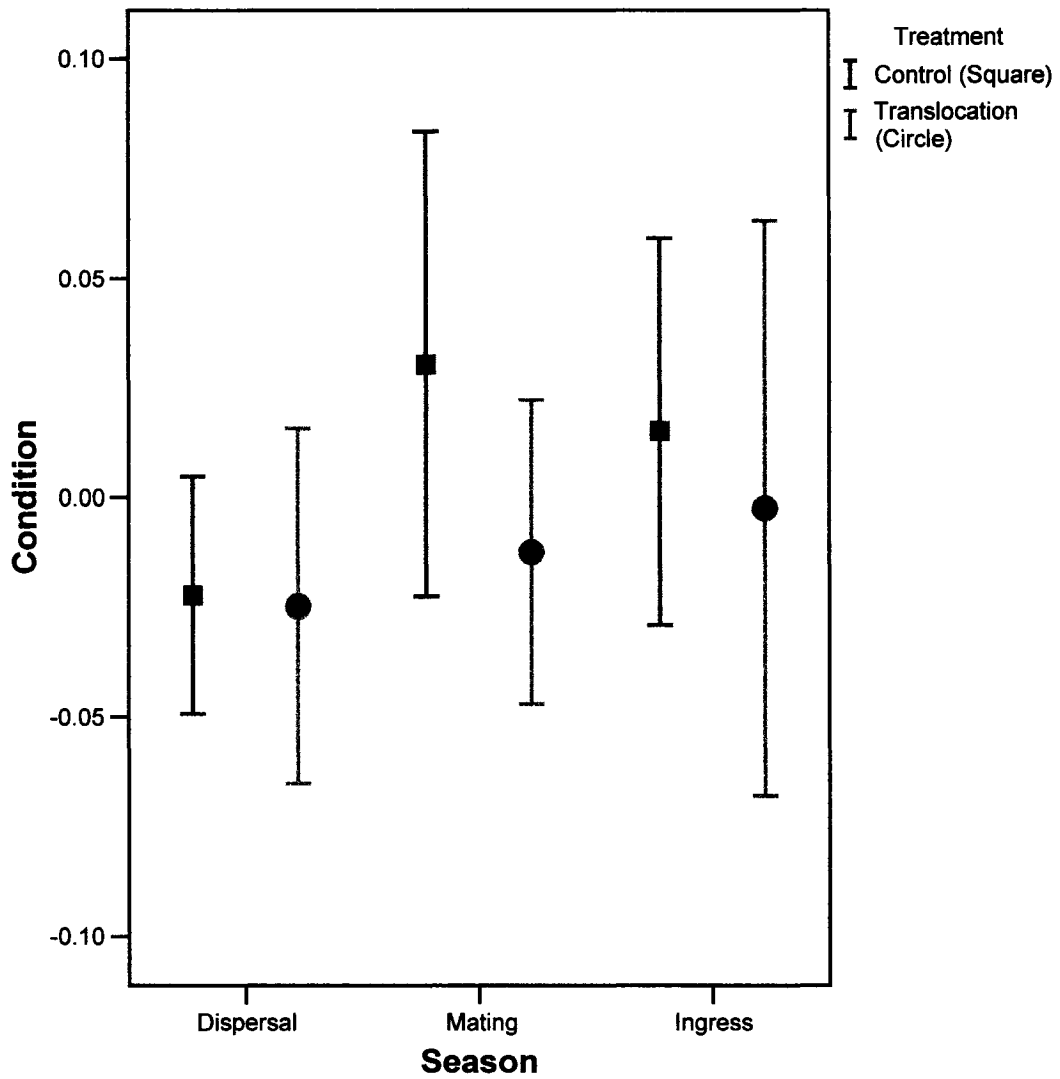


Figure 9: Comparison of the mean body condition, with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments by season.

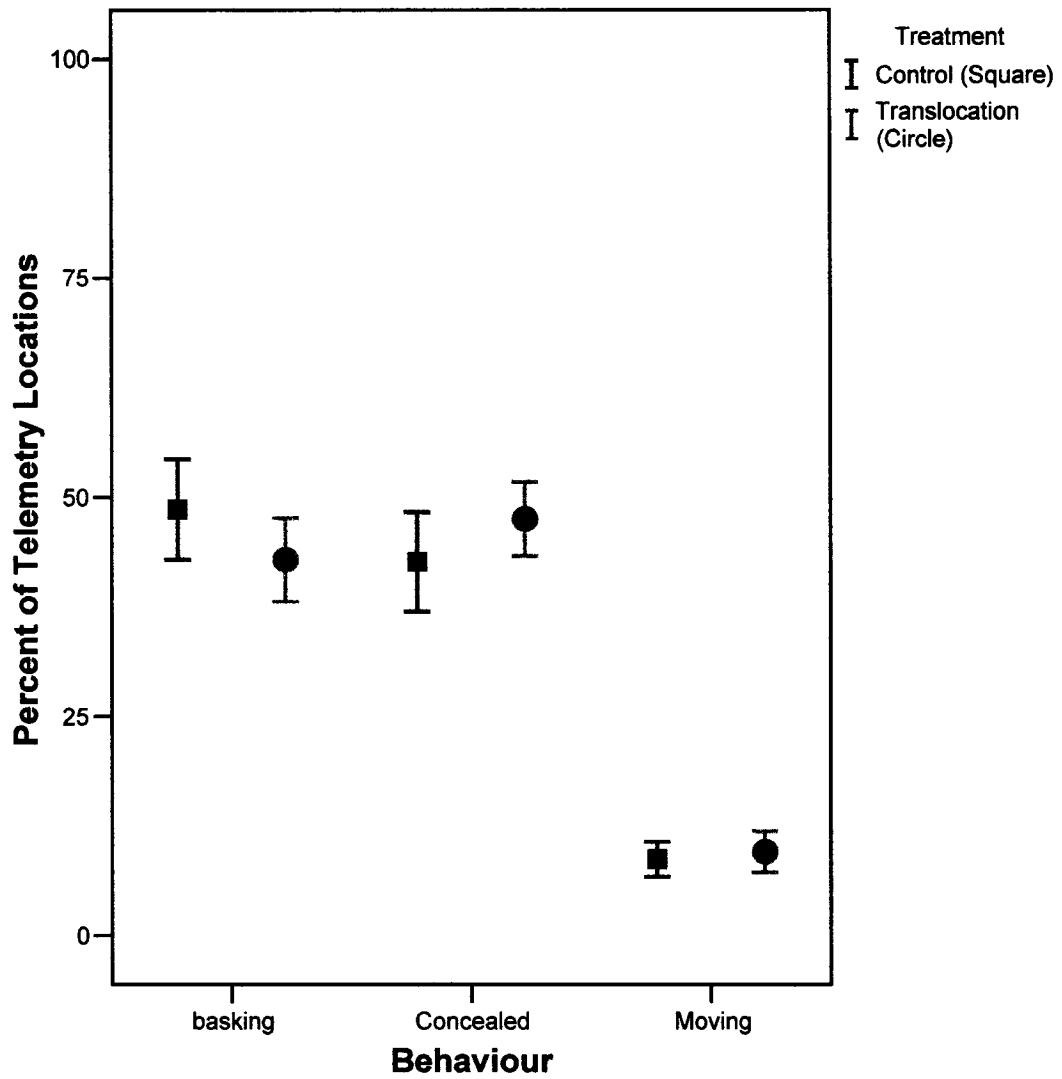


Figure 10: Comparison of the mean percent of telemetry locations where rattlesnakes were found basking, concealed, or moving, with 95% confidence intervals, for Western Rattlesnakes in control and translocation treatments.

Habitat Use

The effect of treatment on the log-ratio transformed habitat use data was not significant ($F_{4,23} = 2.049$, $P = 0.121$). The percent of telemetry locations in each habitat type for rattlesnakes in the control treatment was: shrub-steppe $86.2 \pm 10.7\%$, pine stand $2.0 \pm 4.9\%$, riparian $3.6 \pm 9.0\%$, wetland $1.2 \pm 2.4\%$, and rock-outcrop $6.8 \pm 7.2\%$. For rattlesnakes in the translocation treatment, the percent of telemetry locations in each habitat type was: shrub-steppe $90.1 \pm 17.2\%$, pine stand $1.3 \pm 4.4\%$, riparian $1.8 \pm 2.1\%$, wetland 0% , and rock-outcrop $6.6 \pm 12.1\%$ (Figure 11).

f. Mortality

Two transmittered rattlesnakes were killed by people after translocation. The first mortality occurred on June 12, 2005, 10 days after the snake had been translocated away from the golf course development. This individual was killed by a golfer on a fairway after traveling from his release location in natural habitat back to the golf course development. The second mortality occurred on August 10, 2005, 17 days after translocation from the campground development. This individual was killed and buried by a human at a campsite after traveling from his release location back to the campground development. In addition to the transmittered rattlesnake mortality, a total of 25 human caused snake mortalities were documented in areas of human activity over the course of the study (Appendix B).

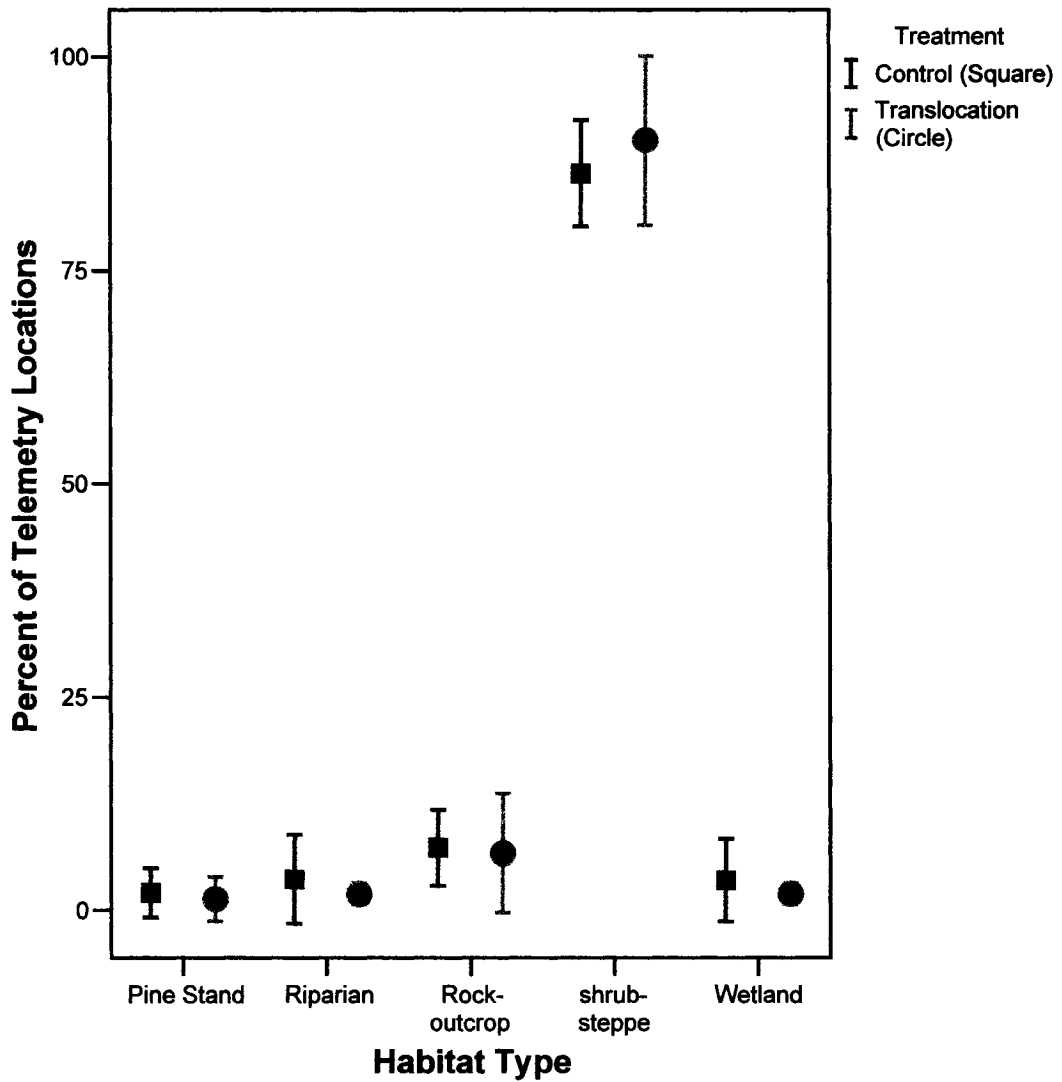


Figure 11: Comparison of the mean percent of telemetry locations, with 95% confidence intervals, in the five major habitat types on the study site for Western Rattlesnakes in control and translocation treatments.

Short-distance Translocation as a Management Tool

a. Full Season Short-distance Translocation

Success Rate of Short-distance Translocation

A total of 47 SDTs were performed on 14 individual rattlesnakes. On average, each individual was translocated 3.4 ± 1.7 times (range 1-7) in a single active season. Only 2 of the 14 SDT individuals were successfully translocated from a management perspective because the snake did not return to an area of human activity in the same active season as the translocation event (Table 3).

Multiple Translocations

For unsuccessful translocations, rattlesnakes returned to an area of human activity within a mean time of 19.9 ± 8.7 days and moved a mean distance of 1167 ± 385 m (Table 3). There was no evidence of a significant relationship between the mean time to return to an area of human activity and the number of translocations per individual ($F_{1,10} = 0.465$, $P = 0.511$, $R^2 = 0.044$). Additionally, there was no significant relationship between the mean distance moved to an area of human activity and the number of translocations per individual ($F_{1,10} = 0.097$, $P = 0.761$, $R^2 = 0.010$).

Site Fidelity

For all unsuccessful translocation events, the mean distance from an individual's previous capture location in an area of human activity was 93 ± 70 m. To determine if rattlesnakes were displaying fidelity to previous capture locations, I tested the distribution of the distance between successive capture locations in an area of human activity in 50m intervals against a null distribution using a chi-square test.

Table 3: Summary information for 14 translocated rattlesnakes, with standard deviations, over the full season, and by dispersal, mating, and ingress seasons.

	Full Season	Dispersal	Mating	Ingress
# of individuals translocated	14	13	9	0
Mean # of translocations/individual	3.4 ± 1.7	2.3 ± 1.4	2.0 ± 0.7	0
# Successful	2	2	0	n/a
Mean time to return to area of human activity (days)	19.9 ± 8.7	25.0 ± 12.3	14.5 ± 8.8	n/a
Mean distance to return to area of human activity (m)	1167 ± 385	1378 ± 470	1108 ± 537	n/a

The distribution of the distances between successive capture locations in an area of human activity were significantly different from a 1:1 distribution ($X^2_{\epsilon} = 20.77$, $P = <0.005$). Post-hoc subdivision of the chi-square analysis revealed the significant deviation from a 1:1 distribution was a result of a significantly higher number of cases in the 0-49m category ($X^2_1 = 3.841$, $P = <0.001$) (Figure 12).

b. Seasonal Short-distance Translocation

Success Rate of Short-distance Translocation

During the dispersal season, 13 individuals were translocated but only 2 were considered successful. On average, rattlesnakes were translocated 2.3 ± 1.4 times (range 1-6). During the mating season, 9 individuals were translocated and none were considered successful. The lack of success in the mating season occurred because individuals were already unsuccessfully translocated during the dispersal season or were translocated multiple times in the mating season. Each individual was translocated, on average, 2.0 ± 0.7 times (range 1-3). No translocations occurred during the ingress season (Table 3). The number of translocations per individual was not significantly different between dispersal and mating seasons ($t_{20} = 0.592$, $P = 0.561$) (Table 3).

Multiple Translocations

During the dispersal season, rattlesnakes translocated more than once, returned to an area of human activity in a mean time of 25.0 ± 12.3 days and traveled a mean distance of 1378 ± 470 m. During the mating season, rattlesnakes returned to an area of human activity in a mean time of 14.5 ± 8.7 days and traveled a mean distance of 1108 ± 533 m (Table 3).

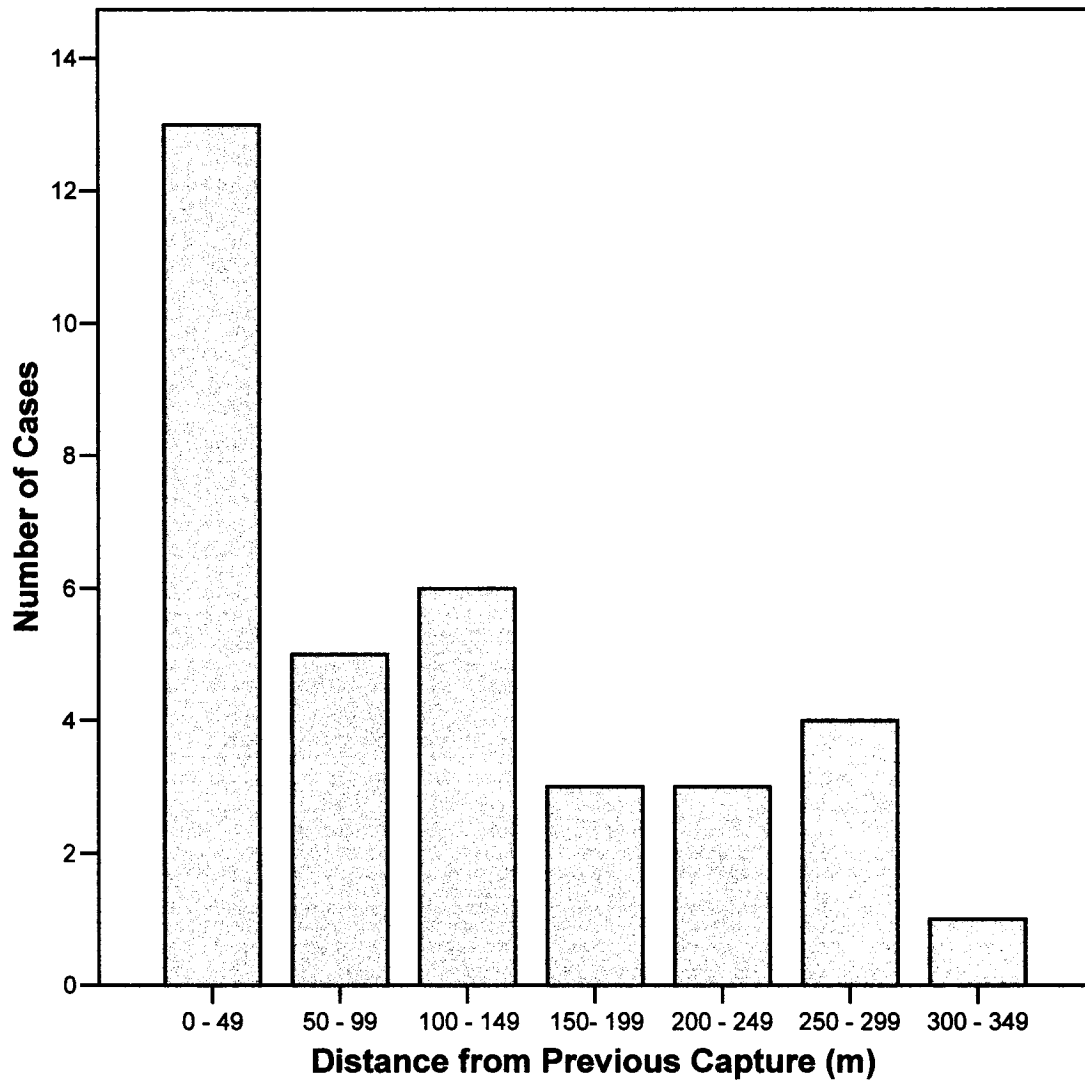


Figure 12: Frequency distribution of the distance from the previous capture location in an area of human activity, in 50m intervals, for unsuccessful translocation events.

There was no significant difference between the dispersal and mating seasons in either the time to return ($t_{16} = 1.953$, $P = 0.069$), or the mean distance to return ($t_{16} = 1.128$, $P = 0.276$) to a previous capture location (Table 3).

DISCUSSION

Effects of Short-distance Translocation

a. Movement Patterns and Activity Range

Previous studies of short-distance translocation (SDT) have not used a handling control to separate potential effects arising from the capture and transportation of rattlesnakes from the effects of SDT on rattlesnake spatial ecology. Separating these effects increases confidence that any observed differences between treatments is due to translocation. I did not detect an effect of handling on movement patterns or size of activity ranges within the control group. Nowak (1997) applied a handling treatment to rattlesnakes in a long-distance translocation (LDT) study and my results were consistent with her study. Because there was no evidence of a handling effect, differences between the control and translocation treatment can be attributed to SDT.

The removal of an individual from its habitat, even to a nearby area, disrupts activity patterns because rattlesnakes rely on specific habitats and locations at different times of the year to carry out biological functions such as hibernation, reproduction and foraging (Macartney 1985; Beaupre 1995; Nowak 1997; Hardy and Greene 1999). Translocated rattlesnakes moved greater total distances than control rattlesnakes. The difference in the total distance moved between treatments occurred because translocated rattlesnakes moved at a higher rate (i.e. further per movement) than control individuals, whereas the frequency of movement did not differ between treatments. Hare and McNally (1997), and Sealy (1997) reported an increase in the total distance moved by rattlesnakes after SDT. However, it is unclear if the increased movement distances observed in these studies arose from elevated rates of movement or increased movement

frequency. The increase in overall movement distances observed in this study is consistent with rattlesnakes undergoing LDT (Nowak 1997; Reinert and Rupert 1999; Plummer and Mills 2000; Butler *et al.* 2005a, 2005b), but a different mechanism caused the difference. Increased movement distances in this study occurred because of multiple unsuccessful translocation events. In LDT studies, increased movements arose from 'wandering behaviour' as individuals attempted to orient themselves in a new environment, often moving in a straight line away from their release site (Nowak 1997; Reinert and Rupert 1999; Plummer and Mills 2000; Butler *et al.* 2005a, 2005b).

I observed a high rate of return to areas of human activity by translocated rattlesnakes which led to multiple translocations on several individuals. I expected these multiple translocations would have a cumulative effect because rattlesnakes are repeatedly removed from their habitat and must continually move to return to these locations. There was a relationship between the total distance moved and the number of translocations per individual, but no relationship between the rate or frequency of movement and the number of translocations per individual over the full active season.

Although SDT affected how rattlesnakes moved through their environment, I did not find strong evidence to suggest translocation altered the space use of Western Rattlesnakes. Range length, range shape, and range size differed little between control and translocation treatments. Activity range sizes obtained in this study for both the translocation and control treatments were relatively consistent with values reported elsewhere for the Western Rattlesnake in British Columbia (Bertram *et al.* 2002). Unlike LDT, SDT did not alter activity range size in snakes (Nowak 1997; Plummer and Mills 2000; Reinert and Rupert 1999; Butler *et al.* 2005a, 2005b). Individuals in LDT studies

did not return to their initial capture areas within a single active season, but did show increased size of activity ranges due to 'wandering behaviour' (Nowak 1997; Reinert and Rupert 1999; Plummer and Mills 2000; Butler *et al.* 2005a, 2005b), presumably while attempting to reach their former activity range. This type of wandering behaviour was likely avoided with SDT because translocated individuals were moved within or very close to their normal activity range.

The typical pattern of rattlesnake movement over an active season consists of infrequent long-distance movements separated by periods of short distance movement during foraging (Macartney *et al.* 1988; King and Duvall 1990; Weatherhead and Prior 1992). Additionally, male rattlesnakes tend to lengthen their movements during discrete mating periods as they actively search for females (Seigel 1986; Reinert and Zappalorti 1988; Brown 1991; Secor 1994; Beck 1995; Duvall 1997). Consistent with these observed increases in movement, rattlesnakes in the control treatment moved at the highest rate and frequency during the mating season, whereas this seasonal trend was not observed within the translocation treatment. The total distance moved did not follow the expected pattern because it was not significantly different between dispersal and mating seasons in the control treatment. However, this trend of increased movement in the dispersal season has been observed elsewhere (Seigel 1986; Beck 1995) and appears to fall within the normal variation of rattlesnake movements. Rattlesnakes in the translocation treatment moved further during the dispersal season than did snakes in the control treatment. A significant number of unsuccessful translocations occurred during this season and they were responsible for increasing movement distances. The rate of movement was higher for the translocation treatment during dispersal, but the difference

was not significant despite an increased total distance moved during this time. The lack of significant difference is likely due to the small sample size (See Appendix C).

No translocations were required during the ingress season because rattlesnakes begin to move towards hibernacula, and areas of rattlesnake-human interaction were restricted to the periphery of the summer activity range far from the hibernacula on the study site. Thus, movement patterns were not affected during ingress. At different locations, translocation may affect movement patterns if the site configuration requires that translocations occur during ingress.

The translocation literature, including this study, tends to focus on adult male rattlesnakes for two reasons. First, methodological constraints (i.e. transmitter size) prevent detailed study of the spatial ecology of juvenile or neonate rattlesnakes. Second, male rattlesnakes tend to move more often than females and juveniles (Macartney *et al.* 1988). It is likely that adult male rattlesnakes are more susceptible to translocation because they spend more energy on movement than females and juveniles and so may be more likely to enter an area of human activity. SDT could potentially be successful for juvenile rattlesnakes if they have not yet established preferred locations within their home range, however, further research is required to test this idea (Heatwole 1977; Reinert 1993). Gravid females may be particularly susceptible to the effects of SDT because they require access to suitable gestation habitat throughout the entire active season to maintain optimal body temperatures. In addition to increasing the movements of gravid females, translocation may prevent females from maintaining optimal body temperatures for incubation, however further research is required to test this idea.

b. Condition, Behaviour, and Mortality

A strong correlation between mass and snout-vent length (SVL) is common in all rattlesnake species (Klauber 1972). As expected, this population of Western Rattlesnakes has a strong positive relationship between mass and SVL which is consistent with previously reported relationships between mass and SVL for Western Rattlesnakes in British Columbia (Macartney 1985).

A decrease in condition was expected after SDT because rattlesnakes spent additional time and energy to return to their pre-translocation areas, which left individuals with less time available for other behaviours such as foraging (Wolf *et al.* 1996). However, I did not detect a significant decline in the condition of translocated rattlesnakes which is consistent with observations in LDT studies (Reinert and Rupert 1999; Nowak *et al.* 2002). During the mating season translocated rattlesnakes had a lower than expected body condition, but this decline was not significant. It is plausible that this trend arose from multiple unsuccessful translocations during the dispersal season, but remained undetected in that season because slow growth rates in adult rattlesnakes (Andrews 1982; Macartney *et al.* 1990) may cause a lag in the response. However, I suspect there was no real difference in condition between treatments for two reasons. First, translocated rattlesnakes effectively navigated to pre-translocation areas when moved with SDT and therefore, did not spend extended periods of time away from preferred locations. Second, individuals were relocated to high quality natural habitat and food quality was likely the same throughout the study area. Despite the increase in movements, rattlesnakes were still able to forage effectively to maintain their body condition in this study area.

To date, no studies have examined the effects SDT has on rattlesnake mating success. Translocation has the potential to reduce mating success in rattlesnakes because individuals move long distances to find females during the mating season (Seigel 1986; Reinert and Zappalorti 1988; Brown 1991; Secor 1994; Beck 1995; Duvall 1997). Translocated individuals moved greater distances because they returned to previous locations in areas of human activity, and there may be a trade off between the time spent mate searching and returning to preferred habitat. Thus, I expected that translocated rattlesnakes would have lower mating success than control rattlesnakes. Studies of LDT have shown translocated rattlesnakes display unusual mating behaviours (e.g. attempted male-male copulation; Reinert and Rupert 1999). However, there was no evidence of a difference in mating success or behaviour between translocation and control treatments. The results do not support the prediction that translocation results in lower mating success in this study area and are inconsistent with the trade-off 'hypothesis'.

When snakes move, they put themselves at an increased risk of predation (Bonnet *et al.* 1999). This risk is often required to satisfy life history functions such as reproduction and foraging (Sealy 1997). I expected that translocated rattlesnakes would have a higher frequency of exposure when compared to control rattlesnakes because translocation caused individuals to move further. Contrary to my prediction, translocated rattlesnakes did not have an increased frequency of exposure compared to the control treatment. Therefore, I found no evidence to suggest the snakes were at a higher risk of predation because they were translocated over a short distance.

An animal's location in a habitat at any point in time is dependent on its current biological needs (Matthiopoulos 2003). I expected SDT would alter habitat use because a

new area is not likely to be ideally suited to a rattlesnake's current needs. Contrary to my expectations, the relative habitat use between control and translocated rattlesnakes was not significantly different. All SDT rattlesnakes were released in the short-shrub habitat, and this habitat contained most of the telemetry locations for both treatment groups. It is possible that the habitat availability is not limited in summer activity areas and prevented any real difference in habitat use. However, the availability of this habitat relative to other habitat types was not quantified and conclusions on habitat selection for the Western Rattlesnake could not be made. When SDT is required in highly fragmented areas, rattlesnakes may not be translocated to ideal habitats. SDT to low quality habitat may affect the condition or vulnerability of rattlesnakes through differential prey or cover object availability, but further research is required to test this idea.

Snakes are typically the top predators where they exist and have relatively low mortality rates in habitats free of human disturbance (Bonnet *et al.* 1999; Reinert and Rupert 1999). However, translocation has resulted in increased mortality rates when using LDT (Reinert and Rupert 1999; Johnson *et al.* 2000; Plummer and Mills 2000) and SDT (Hare and McNally 1997). Incidents of increased mortality after translocation arise from increased predation risk and a decrease in body condition from excess energy expenditure, so I expected to observe increased mortality rates among translocated rattlesnakes because they exhibited an increase in overall movement distances. Two transmittered rattlesnakes were killed while traveling to their original capture location after a translocation event. Although there was no evidence that the stress of translocation increased mortality rates, the mortality observed in this study shows there is a risk to rattlesnakes that occupy areas of human activity. In addition to two

transmitted rattlesnake mortalities, 25 rattlesnakes were killed in areas of human activity (Appendix B). Other studies have found human induced mortality in areas where rattlesnakes and humans co-exist (Rosen and Lowe 1994; Hare and McNally 1997).

I predicted that a disruption in normal activity patterns would result in negative effects on rattlesnake life history. However, this study suggests this was not the case and my prediction was not supported. Rattlesnakes foraged effectively to maintain their body condition after translocation. In addition, SDT did not have an impact on mating success or change their frequency of exposure. I suspect there was no impact on these life history variables because release locations were in high quality habitat similar to initial capture locations which were near or within the snake's normal home ranges. I expected to observe high mortality rates in translocated rattlesnakes because of the combination of a potential for increased energy expenditure and predation risk associated with increased movements. No increased mortality was caused by translocation stress, which suggests snakes can effectively cope with increased movement distances when released in similar high quality habitats. Some human-induced mortality in areas of human activity was documented, showing at least some risk to rattlesnakes in areas of rattlesnake-human interaction. Despite an increase in the total distances moved by translocated rattlesnakes, no evidence of negative effects on rattlesnake life history was detected in this study area.

Short-distance Translocation as a Management Tool

a. Success Rate

Overall, SDT of 500m was not a successful management strategy. Twelve of 14 rattlesnake translocations were unsuccessful because the rattlesnake returned to an area of rattlesnake-human conflict at least once in the same active season. The results support

the prediction that translocation would result in high rates of return to areas of rattlesnake-human conflict. The rate of failure for SDT observed in this study is the highest ever reported. Hardy et al. (2001) reported 36% to 56% of translocated rattlesnakes were recaptured in areas of human activity over two years, and Hare and McNally (1997) and Sealy (1997) reported mere 2% and 4% recapture rates respectively. However, the recapture rates in these studies were likely underestimated because the authors used simple mark and recapture methods rather than radio-telemetry. It is probable some rattlesnakes returned to an area of human activity but remained undetected. Radio-telemetry allowed me to report unbiased rates of return to areas of human activity.

During the dispersal season, rattlesnakes move from their hibernaculum to their summer activity range, and I suspect the low success rate of translocation during this season was because rattlesnakes were translocated while attempting to reach their summer activity area. During the mating season, no translocations were considered successful because individuals were already unsuccessfully translocated in the dispersal season or because individuals were translocated multiple times during the mating season. It appears that individuals were able to home to their specific activity areas, despite multiple SDTs. On this study site, no translocations were required during the ingress season because there were no rattlesnake-human conflict areas near hibernacula. The presence of humans near rattlesnake hibernacula may increase the chance of translocations occurring during the ingress season because individuals may cross these areas as they head for their hibernation site, therefore, the location of rattlesnake-human

conflict areas in the landscape is an important factor in the design of SDT management programs.

b. Multiple Translocations

Studying how rattlesnakes return to an area of human activity after translocation is crucial to form effective management recommendations, but has not been previously reported. Unsuccessful translocation events produced an average of approximately 3 weeks of 'snake free' time in areas of human activity. As rattlesnakes are translocated more often, it is possible they may learn how to return to preferred habitat more effectively. If this is the case, I expected the distance and time required to return to a previous capture location in an area of human activity to decrease as the number of translocations increased, but no relationship between the mean time or distance to return to preferred habitat and the number of translocations was observed. Because the translocation events occurred in a random direction, it is unlikely individuals could have learned to return to their preferred locations more efficiently unless they were familiar with their entire activity range.

Because rattlesnakes are habitual, I predicted individuals would display site fidelity by returning to their pre-translocation locations. In other studies of SDT, rattlesnakes returned to preferred foraging areas after translocation (Hardy et al. 2001). Similarly, this study supported the prediction that rattlesnakes display site fidelity. For unsuccessful translocation events, individuals were recaptured within 50m of their previous capture location in an area of human activity more often than recaptures in any other distance categories up to 350m from the initial capture location. Site fidelity helps to explain the low success rates of SDT for the Western Rattlesnake. Displaced

individuals effectively oriented themselves and navigated to preferred habitat. In addition, site fidelity supports the idea that Western Rattlesnakes make use of preferred locations within their habitat, and the presence of humans in these preferred areas does not appear to deter individuals from utilizing that habitat. SDT was unsuccessful in solving rattlesnake-human conflict because this management strategy is not consistent with the biological needs of the Western Rattlesnake.

Conservation and Management Implications

Increased human presence and development throughout the range of the Western Rattlesnake in British Columbia is responsible for a rising level of rattlesnake-human interaction. These interactions increase the risk of intentional and accidental mortality for rattlesnakes, and may lead to significant population declines. Management strategies need to ensure no harm is done to the resident snakes while at the same time maintaining human safety.

SDT of 500m increased the movements of Western Rattlesnakes, but no evidence of negative effects on their life history was detected. Thus, SDT may be successful from the rattlesnake or conservation point of view because rattlesnakes were able to perform normal life history functions after translocation. Over the short term, SDT likely increased survival rates of individuals by removing them from an area with a potentially increased risk of mortality.

From a management or human safety perspective, SDT was not a successful management strategy. Nearly all translocated rattlesnakes returned to an area of human activity within the same active season as the translocation event. Most translocated individuals needed to be translocated multiple times, up to a maximum of 7 times in one

active season. Rattlesnakes in this population did not display active avoidance of areas of human activity. Such avoidance has been observed in other translocation studies (Sealy 1997). SDT failed as a long-term management tool because it failed to account for the biology of the Western Rattlesnake. The observed site fidelity confirms rattlesnakes rely on specific locations. If rattlesnakes are removed from these locations they have a strong tendency to return and SDT cannot prevent this.

Although the low success rates of SDT prevent it from being used as a stand alone long-term management tool, this technique should not necessarily be abandoned. Previous studies of LDT suggest this management option is inappropriate from a conservation perspective because it has negative effects on spatial ecology, life history and mortality rates in snakes (Nowak 1997; Reinert and Rupert 1999; Johnson *et al.* 2000). In addition, non-removal increases the mortality risk to individuals (Seigel 1986; Brown 1993; Bonnet *et al.* 1999). LDT and non-removal are not viable options to resolve rattlesnake-human conflict if the goal is to maintain rattlesnake and human safety. SDT may solve rattlesnake-human conflict over the short-term by removing the rattlesnake from a potential risk of mortality and removing a potential threat to human safety. Thus, I recommend cautious use of SDT up to a maximum of 500m as part of a rattlesnake management program only if it is viewed as a last resort and short-term solution to rattlesnake-human conflict, rather than a stand alone long-term management strategy. When developing a SDT management program for rattlesnakes, one must take into account several factors including: the biology of the rattlesnake (i.e. habitat requirements and quality of the release site), the site configuration (i.e. location of rattlesnake-human conflict areas in relation to potential hibernacula and summer activity

areas) and the timing of the translocation event (i.e. differential success rates between seasons) in order to be maximally effective. Additionally, it is important to note that further research is required to determine the effects and effectiveness of SDT when used; 1. on juvenile and gravid female rattlesnakes, 2. in fragmented or degraded habitats, and 3. at distances greater than 500m.

If SDT is used as one element of a management strategy it has the potential to be effective. The general public has a lack of understanding of the life history and behaviour of rattlesnakes combined with an unrealistic perception of the danger these timid animals actually pose to people (Greene 1997). This misinformation has led to a general mistrust of rattlesnakes. It is essential for future rattlesnake management programs to include public education aimed at the reduction of intentional and accidental killing of rattlesnakes to reduce the need for SDT, and to reduce the risk to individual rattlesnakes when they eventually return to conflict areas after SDT. In addition, rattlesnake exclusion fencing in areas of intense human use (e.g. campgrounds and parks) has the potential to reduce rattlesnake-human conflict and therefore the need for short-distance translocation. However, rattlesnake exclusion fencing has not been tested. Public education combined with SDT is likely to be maximally effective in mitigating rattlesnake-human interaction from both a conservation and management perspective while other options are investigated. Future study is required to determine if exclusion fencing can provide an effective barrier to heavily used areas of human activity without negative effects on rattlesnake populations.

Conclusions

This research demonstrated that short-distance translocation to high quality habitat free of human disturbance caused Western Rattlesnakes to increase the total distance moved in an active season through increased movement rates. The most significant increase in movement arose from multiple unsuccessful translocation events during dispersal. I suggested that these changes in movements would lead to negative effects on the life history of Western Rattlesnakes. However, translocated rattlesnakes foraged effectively and displayed typical rattlesnake behaviours, despite increased movements. It is also clear that rattlesnakes in areas of human activity have some risk of intentional or accidental human-induced mortality. SDT failed as a long-term management strategy because rattlesnakes tended to display fidelity to specific locations which led to high rates of return to areas of rattlesnake-human conflict and multiple translocations on the same individuals. However, SDT successfully mitigated rattlesnake-human conflict over the short-term.

SDT is a viable short-term solution to rattlesnake-human conflict where the two species interact, and its effectiveness will likely be increased when it is used as a part of a larger management plan. The knowledge that SDT is not a viable long-term solution for the Western Rattlesnake will help shape future rattlesnake conservation and management efforts where rattlesnakes and humans interact.

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APPENDIX A

Table A1: Sample size information for 23 individual rattlesnakes representing 28 full active seasons included in the short-distance translocation analyses.

Snake number	Year	Treatment	Number of translocations	Number of days monitored	Number of tracking locations	Mean tracking interval (days)
1	2004	Control	0	150	72	2.11
2	2004	Control	0	135	64	2.14
3	2004	Control	0	115	51	2.3
4	2004	Control	0	105	50	2.14
5	2005	Control	0	152	65	2.38
6	2005	Control	0	152	63	2.45
7	2005	Control	0	132	51	2.64
8	2005	Control	0	132	50	2.69
9	2005	Control	0	127	54	2.4
10	2005	Control	0	157	69	2.31
11	2005	Control	0	169	70	2.45
12	2005	Control	0	169	70	2.45
13	2005	Control	0	152	64	2.41
14	2005	Control	0	135	59	2.33
15	2004	Translocation	3	149	72	2.1
16	2004	Translocation	2	147	73	2.04
17	2004	Translocation	1	150	73	2.08
18	2004	Translocation	4	130	62	2.13
19	2004	Translocation	3	129	62	2.11
20	2004	Translocation	5	128	66	1.97
21	2004	Translocation	3	122	56	2.22
22	2005	Translocation	6	169	77	2.22
23	2005	Translocation	4	171	76	2.28
24	2005	Translocation	3	171	69	2.51
25	2005	Translocation	2	174	72	2.45
26	2005	Translocation	7	169	73	2.35
27	2005	Translocation	1	166	70	2.41
28	2005	Translocation	3	170	74	2.33

APPENDIX B

Table B1: Summary of the year, location, and cause of 25 Western Rattlesnake mortalities on the study site, collected between April 2004 and October 2005.

Year	Location	Cause of Mortality
2004	Campground	Hit by car
2004	Campground	Hit by car
2004	Campground	Hit by car
2004	Campground	Unknown
2004	Campground	Unknown
2004	Golf Course	Mower
2004	Golf Course	Mower
2004	Golf Course	Intentional by human
2004	Road	Hit by car
2004	Road	Hit by car
2004	Road	Hit by car
2005	Campground	Hit by car
2005	Campground	Hit by car
2005	Campground	Hit by car
2005	Campground	Hit by car
2005	Campground	Intentional by human
2005	Campground	Intentional by human
2005	Golf Course	Mower
2005	Golf Course	Intentional by human
2005	Road	Hit by car
2005	Road	Hit by car
2005	Road	Hit by car
2005	Road	Hit by car
2005	Road	Hit by car

APPENDIX C

Table C1: Power analysis for all variables and their statistical tests included in the short-distance translocation data analyses. Power values are based on the ability to detect a ‘large’ effect size following the methods of Cohen (1977) and an alpha of 0.05.

Variable	Statistical Test	Sample Size	Power
All full season movement and activity range variables	ANCOVA	28	0.5312
	linear regression	14	0.5300
All seasonal movement variables	MANOVA with repeated measures	28	between subjects 0.8538 within subjects 0.7824
	linear regression	13	0.4945
Condition	MANOVA with repeated measures	17	between subjects 0.6260 within subjects 0.5353
Mating success	t-test	28	0.6614
Frequency of exposure	MANOVA	56	0.8364
Habitat use	MANOVA	112	0.9513
Site fidelity	chi-square	35	0.8409
Seasonal success rates of translocation	t-test	22	0.5545
Mean distance and mean time to return to an area of human activity	linear regression	11	0.4182

* All power analyses were conducted using the computer program GPOWER (Faul and Erdfeller 1992)