Anthropogenic disturbance increases movement and crypsis in western diamond-backed rattlesnakes (Crotalus atrox)

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April 2014

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II. ABSTRACT

Anthropogenic disturbance contributes to reptile endangerment, but few studies have examined the interactions between reptiles and humans. The purpose of my study was to examine how anthropogenic disturbance affects the movements and behaviour of western diamond-backed rattlesnakes at the Arizona-Sonora Desert Museum near Tucson, Arizona. I hypothesized that disturbance would have a significant effect on movement and behaviour. I predicted that rattlesnakes would have a higher probability of movement and be less visible in highly disturbed areas. Twenty-five snakes were captured opportunistically on museum grounds between July 2005 and September 2011 and were fitted with radio-transmitters. Snakes were tracked a minimum of twice weekly. During the mating and active seasons, snakes were significantly more likely to move and remain concealed in highly disturbed areas. During the inactive season, disturbance had no significant effect on the probability of movement and on behaviour. Disturbance also has no significant effect on distance moved. Regardless of season, when snakes are in highly disturbed areas, they are significantly more likely to remain non-visible. The outcomes of my analyses provide support for my hypotheses, indicating that anthropogenic disturbance has an effect on the movement and behaviour patterns of western diamond-backed rattlesnakes.

III. ACKNOWLEDGEMENTS

I would like to thank my supervisor, Gabriel Blouin-Demers, for introducing me to research and always being ready to answer my questions. I would like to thank Bill Halliday for his assistance with R software and my statistical analyses. I would also like to thank James Paterson for his assistance with ArcGIS and my spatial analyses. Lastly, I would like to thank the Arizona-Sonora Desert Museum for providing me with several years worth of data on western diamond-backed rattlesnakes and for answering my questions.

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VII. INTRODUCTION

The extinction of species is increasing globally in large part due to habitat degradation, fragmentation, and destruction (Gibbons 2000). By expanding roads, converting forests, rerouting water, draining wetlands, and introducing pollution, humans negatively alter pristine habitats. Specifically, Dobson *et al.* (1997) found that agricultural output is highly correlated with the overall density of endangered species in the United States. Some models predict that averaged across all biomes, land-use change is the single greatest driver expected to impact global biodiversity by year 2100 (Sala *et al.* 2000). Land-use change is projected to have a large impact because it reduces habitat availability and habitat quality, leading to species extinction (Sala *et al.* 2000). Further, as human encroach on natural land, the presence of humans may also directly and indirectly impact global species decline.

As human population is increasing at unprecedented rates, human interactions with wildlife are also increasing. These interactions include direct and indirect anthropogenic disturbances to wildlife. Direct anthropogenic disturbance is caused solely by the presence of humans in nature. Indirect anthropogenic disturbance refers to habitat alterations as a result of human presence, including alteration from construction, settlement, and transportation (Ohashi *et al.* 2013). Federal legislation in Canada and the USA already exists to protect species from both direct and indirect human disturbance. Specifically, clause 32(1) of the Species at Risk Act of Canada and section 9a(1)(B) of the Endangered Species Act of the USA both prohibit the harming, harassing, and capturing of listed species. Further, clause 58(1) of the Species at Risk Act and section 9a(1)(G) of the Endangered Species Act states that the destruction of critical habitat of listed species is forbidden. However, tourism and outdoor recreational activity introduce anthropogenic pressure to wildlife and pose a threat to global biodiversity (Rodriguez-Prieto & Fernandez-Juricic 2005).

The short and long-term effects of anthropogenic disturbance must be identified to understand how these effects influence species decline. Studies have shown that human disturbance significantly alters behaviour (Ohashi *et al.* 2013, Ciuiti *et al.* 2012, Burger 1994), abundance (Rodriguez-Prieto & Fernandez-Juricic 2005), habitat selection (Liley & Sutherland 2007), and reproductive success (Carney & Sydeman 1999) of vertebrate species. Specifically, Ciuiti *et al.* (2012) found that during increased human hunting activity, elk exhibited a significant increase in vigilance behaviour, which, consequently, was related to a decrease in foraging behaviour. In the long term, decreased foraging behaviour can be detrimental as it may reduce physiological health and increase mortality. Further, Rodriguez-Prieto and Fernandez-Juricic (2005) found that the abundance of Iberian frogs decreased by 80% when the number of human visitors increased five times. A reduction in abundance may also be detrimental to the survival of this species. Lastly, Carney and Sydeman (1999) reviewed the impact of human disturbance on nesting colonial waterbirds and found that scientific investigators have significant impacts on reproductive success. A drop in reproductive success may have adverse effects on the persistence of these species in the long term. Clearly, human disturbance negatively affects many vertebrates.

Human disturbance also contributes to reptile endangerment. Studies show that reptiles are less abundant in disturbed habitats (Brown 2001) as reptiles may evade the increased human presence in disturbed locations. Further, Ficetola *et al.* (2007)

found that disturbance by humans negatively affected the presence of wall lizards and western whip snakes. This same study shows that human disturbance also significantly reduced reptile species richness (Ficetola *et al.* 2007). Additionally, a study was conducted in North Carolina, USA to describe the behaviour of timber rattlesnakes in Hanging Rock State Park (Sealy 2002). Sealy (2002) found that one of the radio-tracked male snakes avoided roads, picnic areas, and parking lots. Furthermore, Nowak *et al.* (2002) studied two separate western diamond-backed rattlesnake populations in Arizona, USA. Results indicate that mortality of rattlesnakes at the Tucson site was higher, likely due to the high degree of human encroachment at this site (Nowak *et al.* 2002). Although the results of this study (Nowak *et al.* 2002) are certainly relevant, the study has poor inferential power, as it compares a single urban site with a single natural site (Garland 1994). Nowak *et al.* (2002) and Sealy (2002) provide examples of how human presence may contribute to reptile endangerment by negatively altering movement patterns and reducing individual snake survival.

The available scientific literature addressing the separate effects of direct human disturbance and indirect human disturbance on wildlife is lacking. Sufficient literature exists evaluating the effect of indirect disturbance on wildlife. However, very few studies focus on the combination of direct and indirect human disturbance; even fewer studies focus solely on direct human disturbance. Several studies presented here examine the effect of human disturbance, but most fail to distinguish whether the effect is solely related to direct human disturbance or solely related to indirect human disturbance. For example, Liley and Sutherland (2007) determined that the site quality and the total number of people present, together, predict the occupancy of nesting ringed plovers 80% of the time. This particular study, among many others, does not distinguish between the effect of site quality (an indicator of indirect human disturbance) and the effect of human abundance (an indicator of direct human disturbance). Moreover, the effects of direct human disturbance and indirect human disturbance are not independent in Sealy's (2002) analysis. It is difficult to disentangle whether direct or indirect human disturbance, or some combination of both, elicited the avoidance behavior of the male snake to man-made structures.

In the case of our particular study, it is very difficult to disentangle the effects of direct and indirect anthropogenic disturbance. Thus, our study will address the collective definition of anthropogenic disturbance, without differentiating between direct and indirect. We hypothesize that movement and behaviour patterns of western diamond-backed rattlesnakes are affected by anthropogenic disturbance. We predict that western diamond-backed rattlesnakes will have a higher probability of movement in areas where there is more anthropogenic disturbance. We also predict that western diamond-backed rattlesnakes will be less visible when in areas with more anthropogenic disturbance.

Our study has further importance because interactions between reptiles and humans are not widely studied. However, the available literature indicates that these interactions are common and can alter defensive behaviour in reptiles. Reptiles can be found in close proximity to human establishments, which increases the probability of human-reptile interactions and reptile habituation. In one particular study, more than 50% of the rattlesnakes hibernated in dens less than 100 meters from a main visitor trail (Nowak *et al.* 2002). Understanding how reptiles behave in these scenarios is important as it can help predict how reptile behaviour will change as human disturbance increases. Specifically, in separate studies, Glaudas (2004) and Glaudas *et al.* (2006) found that when adult cottonmouths are handled more frequently, snakes exhibit significant decreases in defensive behaviour. Furthermore, habituation can be beneficial for reptiles because it allows reptiles to maintain a higher body condition in the constant presence of low-risk predators (Rodriguez-Prieto *et al.* 2010). Therefore, not only does human disturbance create the potential for species decline, but it also creates the potential for altered reptile behaviour.

Understanding the effect of human disturbance on the behaviour and movements of reptiles is also vital for conservation. It is important to understand how human disturbance impacts reptile populations because these interactions can govern how conservation policy and management is created. For example, in Hanging Rock State Park, one hiking trail was closed in an effort to reduce human traffic through a timber rattlesnake gestation site (Sealy 2002). Thus, by understanding rattlesnake movement and behaviour patterns, management practices can be implemented to protect natural habitat from disturbance by humans.

VIII. MATERIALS AND METHODS

Study Area

The Arizona-Sonora Desert Museum (ASDM) is located approximately 19 km west of Tucson, Arizona in the mountainous desert scrub (32°14’ N, 111° 10’ W) (Appendix 1.1). The ASDM is located within the Tucson Mountain Park, a natural resource area managed by the local government. Although the ASDM grounds are 40 ha, the area considered for this study is approximately 125 ha. The study area includes the ASDM grounds, as well as some surrounding land in the Tucson Mountain Park. The museum attracts between 450 000 and 500 000 visitors annually. Further, five species of rattlesnake are found on the museum grounds (*Crotalus atrox, C. cerastes, C. molossus, C. scutulatus* and *C. tigris)* and human-rattlesnake encounters are common.

Study Animals

Fifteen male western diamond-backed rattlesnakes (*Crotalus atrox*) were captured between July 2005 and June 2007, and ten females were captured between March 2008 and September 2011 (Appendix 1.2). Snakes were captured opportunistically on the museum grounds. From July 2005 to July 2010, we followed the fifteen males via radio-telemetry for periods ranging 73 days to 1773 days. From March 2008 to May 2013, we followed the ten females via radio-telemetry for periods ranging from 47 days to 777 days.

Radio-telemetry

All snakes were weighed, sexed and marked as outlined by Johnson *et al.* (2002). All rattlesnakes were fitted with 13 g transmitters with a battery life of 24 months at 35°C (50mm x 11mm, SI-2T Holohil Systems Incorporated, Carp, Ontario). Radiotelemetry coelomic implant surgeries were performed in a sterile surgical field, as outlined by Weatherhead and Blouin-Demers (2004). Identical surgical approaches and procedures were followed to replace and remove transmitters at later dates. Once released, the radio-tracked rattlesnakes were located a minimum of two times weekly, using an AVM LA12-Q radiotelemetry receiver and a collapsible Yagi antennae. Data on snake location and snake behaviour was recorded. All locations were recorded using a global positioning system (GPS) unit (Garmin 12 XL 12, 1-2 meters accuracy). The Universal Transverse Mercator coordinates (North American Datum of 1983, Zone 12N) of each location were used for spatial analyses.

Spatial Analyses

ArcGIS (Environmental Systems Research Institute (ESRI) Inc. 2013) was used for spatial analyses of snake movements. *Hawth's Tools* (Beyer 2004) was used to calculate distance moved (in meters), for each individual snake, between subsequent radio-tracked locations. These data were used to generate the distance moved variable. A total of 2332 radio-tracked locations were recorded for this study, with the fewest radio-tracked locations for an individual snake being 12 and the greatest radio-tracked locations for an individual snake being 272. Distances of four meters and under were considered "no movement" and received a category of 0. Distances of five meters and over were considered "movement" and received a category of 1. These data were used to generate the probability of movement variable.

Google Earth (Google Inc. 2013) was used to determine polygons of differing disturbance levels for the study area (Fig. 1). A map of the ASDM grounds (Appendix 1.3) was also used for cross-referencing to determine disturbance polygons.

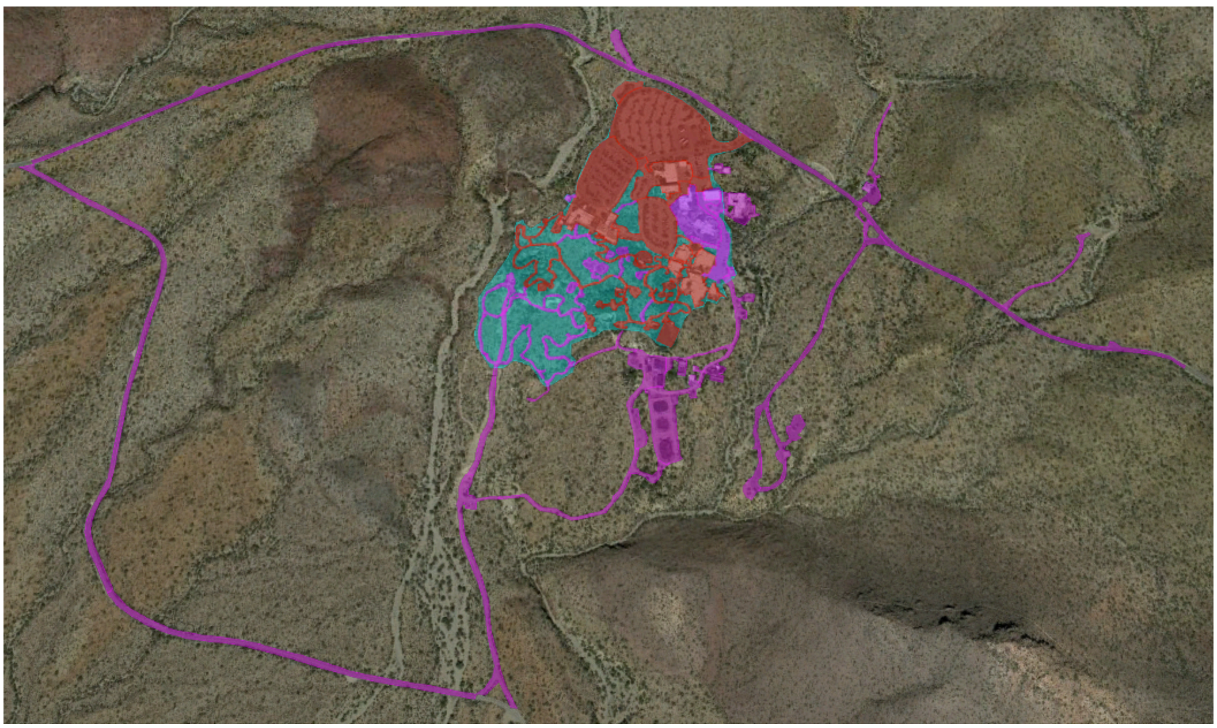


Figure 1. Disturbance zones at the Arizona-Sonora Desert Museum, as classified by *Google Earth*. Blue represents the public ASDM grounds, red represents Level 3 disturbance zones, and pink represents Level 2 disturbance zones. Level 1 and Level 0 disturbance zones were classified in *ArcGIS* using the zones indicated in the figure.

Disturbance Level 3 is classified as any areas on the ASDM grounds that include buildings open to the public, paved paths, parking lots, stairs, restrooms, drinking fountains, smoking areas, first aid areas, and any shade areas accessible by a Level 3 path. Disturbance Level 2 is classified as any areas on the ASDM grounds that include buildings open only to maintenance staff, dirt paths, bridges, underground tunnels, and any shade areas accessible by a Level 2 path. Disturbance Level 2 is also classified as human establishment areas off ASDM grounds, within the study area. A polygon was then created to outline the ASDM public grounds using *Google Earth* (the blue area in Figure 1). ASDM public grounds, Disturbance Level 3, and Disturbance Level 2 polygons were then imported into *ArcGIS* in order to create Disturbance Level 1 and Disturbance Level 0 polygons, using the Erase Tool. Disturbance Level 1 is classified as any area within the ASDM public grounds that is not classified as Disturbance Level 2 or 3. Disturbance Level 0 is classified as any area off ASDM public grounds, within the study area, that is not classified as Disturbance Level 2.

Once disturbance polygons were created in *ArcGIS*, the Buffer Tool was used to apply two meter, five meter, and ten meter buffers on all disturbance layers (Level 3, Level 2, Level 1, and Level 0). When a buffer from one layer (i.e.: Level 2) overlapped with a buffer from another layer (i.e.: Level 3), the more disturbed layer (i.e.: Level 3) always took precedence (Appendix 1.4). Five meter buffers were used for the main statistical analyses of this study because a five meter buffer distance was deemed to be most biologically relevant to the study animals. The GPS unit is only accurate to 1-2 meters, which suggests a two meter buffer may to be too strict. A ten meter buffer may be too generous, as highly disturbed areas may not actually have a surrounding biological effect of ten meters. Lastly, despite the differences in buffer distance, all analyses produced generally quantitatively similar results, with few minor anomalies (see Appendix 1.5 for comparison of results based on buffer width).

Using the buffered disturbance layers, the Select By Location tool in *ArcGIS* was used to assign radio-tracked locations to a disturbance level. Using the layers with five meter buffers, 439, 410, 254, and 1230 radio-tracked locations were assigned Disturbance Level 3, Level 2, Level 1, and Level 0, respectively (see Appendix 1.5 for two meter and ten meter buffer results). These data were used to generate the disturbance variable.

Behaviours of snakes recorded at each radio-tracked location were classified as either "non-visible", "visible stretched", "visible partial coil", and "visible full coil", and received an ordinal variable of A, B, C, or D, respectively. These data were used to generate the behaviour variable. Behaviour was classified on an ordinal scale because the behaviour logically flows from concealed and cryptic behaviours to to non-concealed and non-cryptic behaviours, in the order listed above. Visibility behaviour of snakes was also determined. Snakes that were classified as "visible stretched", "visible partial coil", or "visible full coil" were all considered "visible" and received a category of 1. "Non-visible" snakes received a category of 0. These data were used to generate the probability of visible behaviour variable.

Statistical Analyses

Four analyses were carried out using *R* software (R Core Team 2013). Specifically, disturbance was compared with probability of movement, distance moved, behaviour, and probability of visible behaviour using logistic regression (Bates *et al.*

2013), linear mixed effects modeling (Bates *et al.* 2013), ordinal logistic regression (Venables & Ripley 2002), and logistic regression, respectively. A total of 2308 and 1683 data points were used for the probability of movement and distance moved analyses, respectively. A total of 2249 data points were used for the behaviour and probability of visible behaviour analyses, each. It is important to further examine distances moved subsequent to probability of movement because for the same probability of movement, snakes may move vastly different distances.

Prior to model selection for each of the four analyses, AIC values were compared for preliminary models to determine which random effects to include in the subsequent models. The random effect of individual must be controlled for because some individual rattlesnakes may have an innate tendency to move or behave differently than others. Sex must also be controlled for because movement patterns may differ between male and female snakes. Further, sex must be controlled for because of the sexual dimorphism in this species, with respect to mass. The mean mass for female snakes is 392 g (±16 g, n = 10) and the mean mass for male snakes is 577 g (± 45 g, n =15), indicating that males are heavier than females. Further, sex and mass are highly correlated (Appendix 1.6), so only one of these variables should be controlled for in the analysis. As mass is presumably determined by sex, we chose to control for sex instead of mass, as sex is most relevant. Additionally, seasonality must be controlled for in this analysis, since mean distance moved per week fluctuates depending on the season (Fig. 2). Mean frequency of movement per week does not fluctuate depending on the season (Appendix 1.7) and was not enough to determine seasonality.

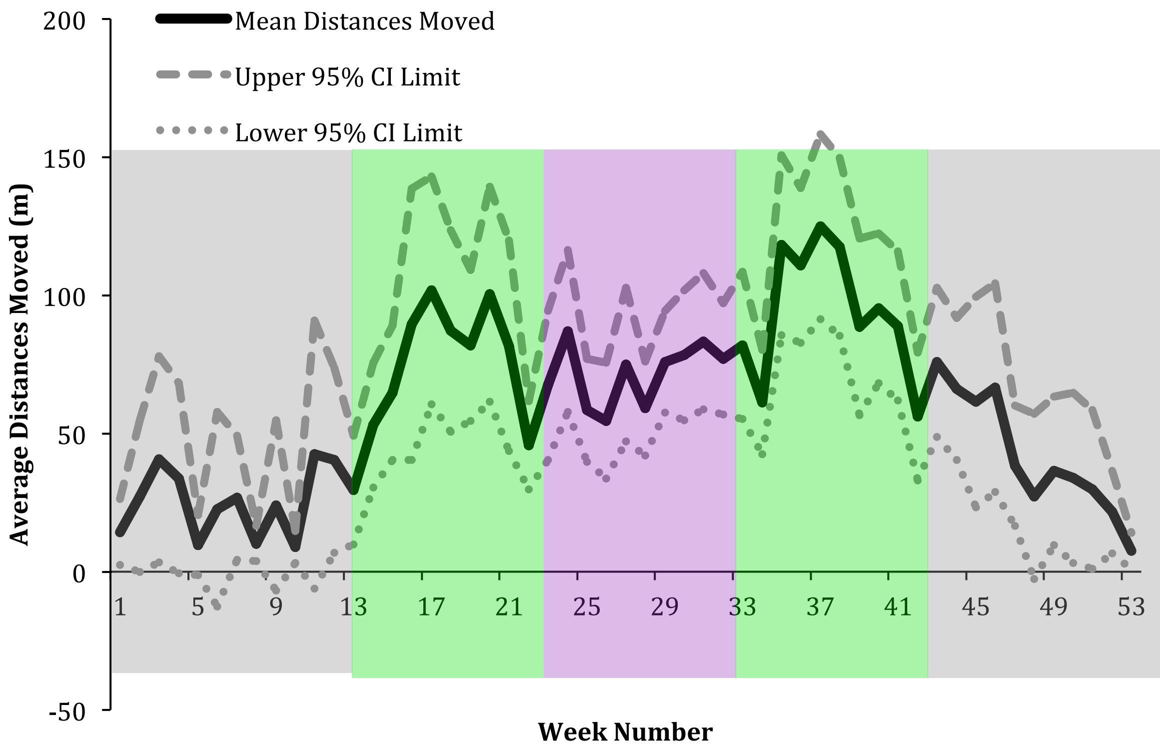


Figure 2. Mean distance moved (meters) per week and 95% confidence intervals (CI). Mean distance moved was determined by averaging the distance moved, across all individual snakes, per week. Seasons are approximately represented by coloured boxes. The inactive season is represented by a grey box (approx. October 20 – March 30), the two mating seasons are represented by green boxes (approx. March 31 – May 25; August 18 – October 19), and the active season is represented by a purple box (approx. May 26 – August 17). The upper (grey dashed line) and lower (grey dotted line) 95% confidence intervals of the mean distances moved are presented.

Both temperature and season could not be included as fixed effects in the models, as temperature fluctuates depending on the season (they are collinear), as determined by preliminary analyses in *R*, and presented in Figure 3. It is apparent when comparing season and temperature in Figure 3 that the temperature is generally hotter during the two mating seasons and the active season. Thus, a preliminary analysis (Appendix 1.8) determined that a model only considering season had a lower AIC value compared to a model only considering temperature, despite the season model having more parameters. This indicates that season explains more variation; therefore, season was chosen for future use in all statistical analyses and temperature was excluded.

After selecting which random effects to include for each analysis, complete models were created with disturbance level, sex, season, and all combinations of interaction terms included as the fixed effects. From these preliminary complete models, least significant parameters were removed until a final model, with the lowest AIC value, was reached. If significant interaction terms between disturbance and season remained in the final model, this was addressed by conducting the same analysis, but separately for each individual season. There are 622, 893, and 794 observations for the active season, mating season, and inactive season, respectively.

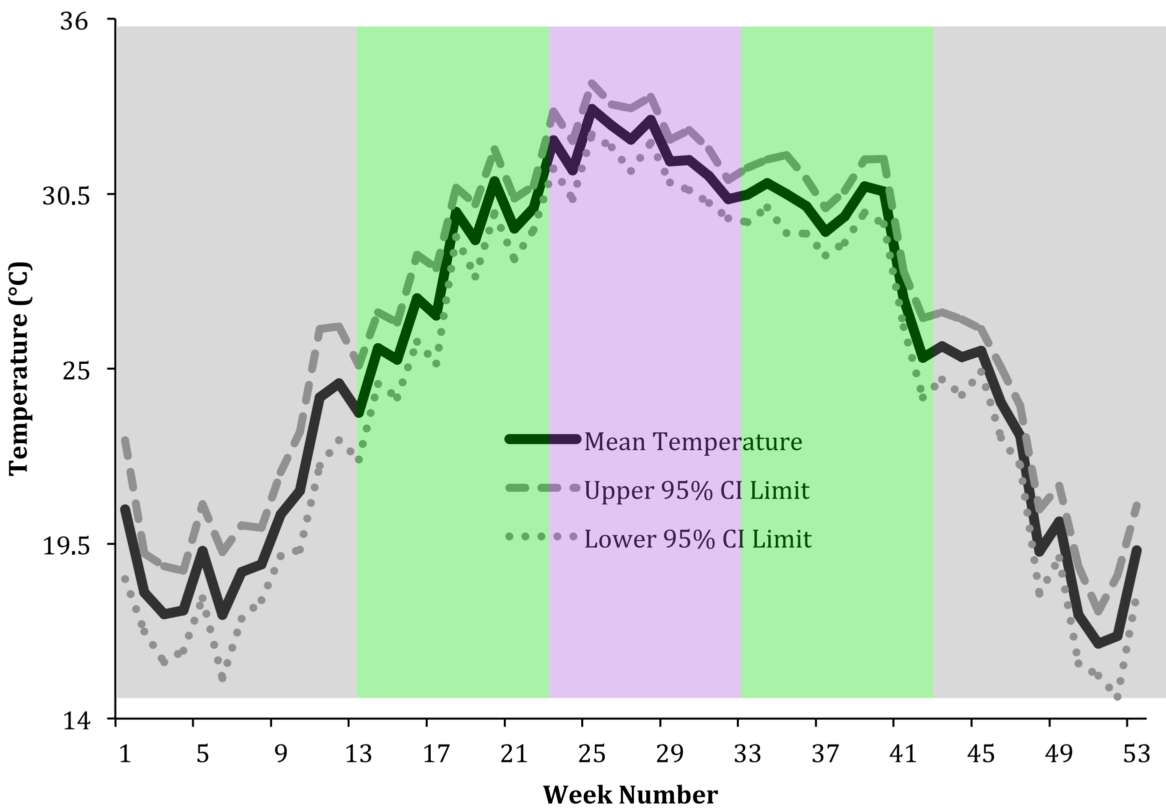


Figure 3. Mean temperature (°C) per week and 95% confidence intervals (CI). Mean temperature was determined by averaging the ambient temperature across all study years. Seasons are approximately represented by coloured boxes. The inactive season is represented by a grey box (approx. October 20 – March 30), the two mating seasons are represented by green boxes (approx. March 31 – May 25; August 18 – October 19), and the active season is represented by a purple box (approx. May 26 – August 17). The upper (grey dashed line) and lower (grey dotted line) 95% confidence intervals of the mean temperatures are presented.

IX. RESULTS

The results presented here are for the disturbance zones determined by the five meter buffer zone. Results for analyses conducted with a two meter and ten meter buffer zone are quantitatively similar and can be found in sections 1.9 and 1.10 of the Appendix.

Probability of Movement

The best model for the probability of movement vs. disturbance analysis indicated a significant interaction between season and disturbance ($p = 0.001$) (Table I). Separate analyses, using the bolded model in Table I, were conducted for each season (Fig. 4, Appendix 1.10). During the mating and active seasons, snakes are significantly more likely to move in highly disturbed areas ($p = 0.03$, $p = 0.042$, respectively). During the inactive season, disturbance is not a significant predictor of probability of movement ($p > 0.05$).

Distance Moved

The best model for this analysis does not include disturbance as a predictor variable (Table II). Thus, disturbance is not a significant predictor of distance moved ($p > 0.05$).

Behaviour

The best model for this analysis includes an interaction between disturbance and season ($p = 0.015$) (Table III). Separate analyses, using the bolded model in Table III, were conducted for each season (Fig. 5, Appendix 1.10) During the mating ($p = 0.0015$) and active seasons ($p < 0.0001$), snakes are significantly more likely to be concealed in highly disturbed areas and to be non-concealed in undisturbed areas.

Table I. Model selection (top panel) and details of the final model (bottom panel) for probability of movement of western diamond-backed rattlesnakes in areas of varying disturbance levels. *k* = the number of parameters in the model, AIC = Akaike's information criteria value, and ΔAIC = difference between AIC values for the best model (bolded) and each other model.

Model	***k***	**AIC**	**ΔAIC**
Random Effects Included For Models Below	*(1 + Season + Sex | Individual)*		
Probability of movement = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season + Disturbance : Sex : Season	22	2427.35	5.87
Probability of movement = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season	20	2426.55	5.07
Probability of movement = Disturbance + Sex + Season + Disturbance : Season + Sex : Season	19	2425.01	3.53
Probability of movement = Disturbance + Sex + Season + Disturbance : Season	17	2423.28	1.80
Probability of movement = Disturbance + Season + Disturbance : Season	**16**	**2421.48**	**0**
Coefficient	**Value (SE)**	**DF**	**p**
Intercept	2.17 (0.25)	2292	< 0.0001
Disturbance	-0.20 (0.11)	2292	0.058
Season (Inactive)	-1.84 (0.29)	2292	< 0.0001
Season (Mating)	-0.71 (0.28)	2292	0.011
Disturbance : Season (Inactive)	0.25 (0.13)	2292	0.057
Disturbance : Season (Mating)	0.45 (0.14)	2292	0.001

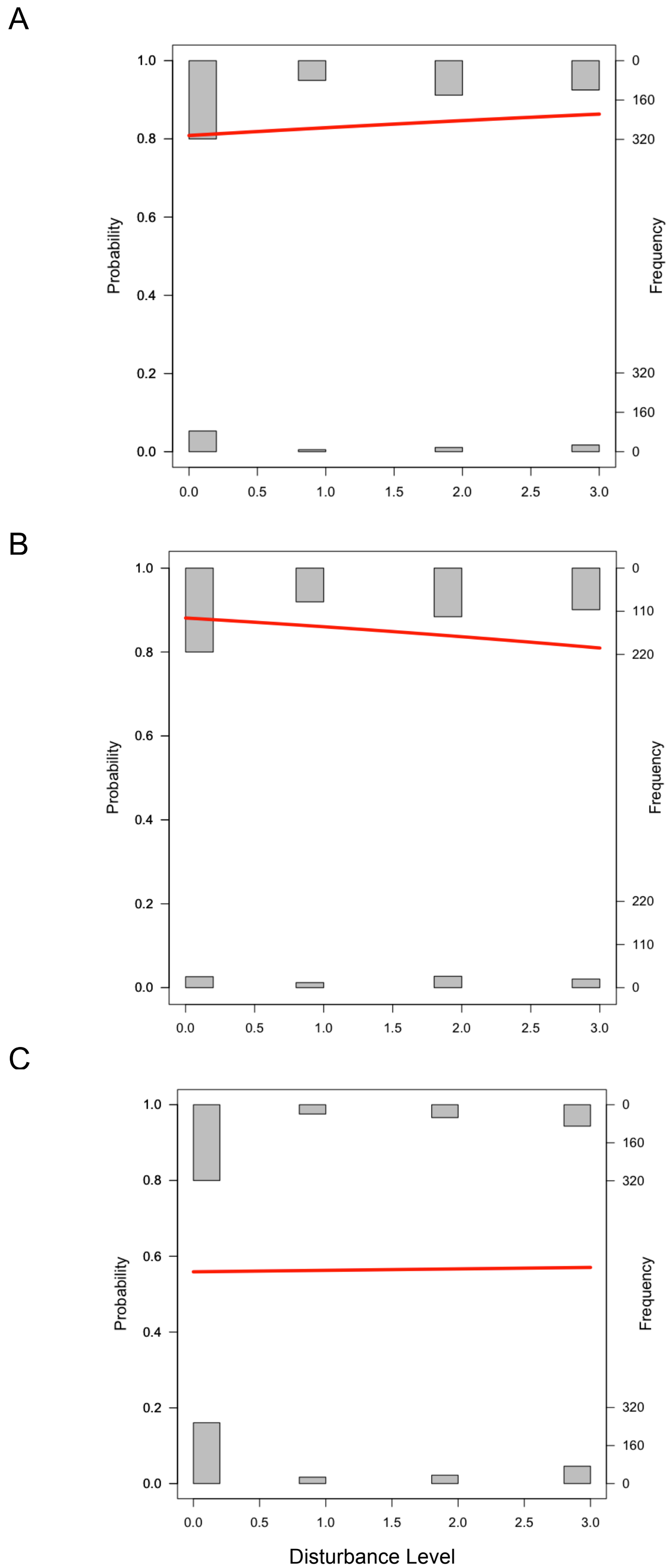


Figure 4. Frequency of observed data (histograms) and probability of western diamond-backed rattlesnake movement as disturbance increases (from Class 0 to Class 3) for mating season (A), active season (B), and inactive season (C), where 0 = no movement, 1 = movement.

Table II. Model selection (top panel) and details of the final model (bottom panel) for log (distance moved) of western diamond-backed rattlesnakes in areas of varying disturbance levels. *k* = the number of parameters in the model, AIC = Akaike's information criteria value, and ΔAIC = difference between AIC values for the best model (bolded) and each other model.

Model		**k**	**AIC**	**ΔAIC**
Random Effects Included For Models Below		*(1 + Season | Individual)*		
Log (Distance Moved) = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season + Disturbance : Sex : Season		19	5478.56	32.78
Log (Distance Moved) = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season		17	5470.34	24.56
Log (Distance Moved)= Disturbance + Sex + Season + Disturbance : Sex + Sex : Season		15	5459.34	13.56
Log (Distance Moved) = Disturbance + Sex + Season + Sex : Season		14	5455.07	9.29
Log (Distance Moved)= Sex + Season + Sex : Season		13	5449.96	4.18
Log (Distance Moved)= Sex + Season		11	5450.27	4.49
Distance Moved = Season		**10**	**5445.78**	**0**
Coefficient	**Value (SE)**	**DF**	**t**	**p**
Intercept	0.12 (0.35)	1673	41.84	<0.0001
Season (Inactive)	-0.71 (0.15)	1673	-4.64	<0.0001
Season (Mating)	0.27 (0.13)	1673	2.02	0.044

Table III. Model selection (top panel) and details of the final model (bottom panel) for behaviour of western diamond-backed rattlesnakes in areas of varying disturbance levels. *k* = the number of parameters in the model, AIC = Akaike's information criteria value, and ΔAIC = difference between AIC values for the best model (bolded) and each other model.

Model		k	AIC	ΔAIC
Behaviour = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season + Disturbance : Sex : Season		15	4310.90	9.08
Behaviour = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season		13	4307.55	5.73
Behaviour = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season		11	4304.35	2.53
Behaviour = Disturbance + Sex + Season + Disturbance : Season		10	4303.65	1.83
Behaviour = Disturbance + Season + Disturbance : Season		**9**	**4301.82**	**0**
Coefficient	**Value (SE)**	**DF**	**t**	**p**
Disturbance	-0.30 (0.07)	2240	-4.24	<0.0001
Season (Inactive)	-1.33 (0.15)	2240	-8.81	<0.0001
Season (Mating)	-0.08 (0.15)	2240	-0.53	0.596
Disturbance : Season (Inactive)	0.23 (0.10)	2240	2.43	0.015
Disturbance: Season (Mating)	0.09 (0.09)	2240	0.93	0.352

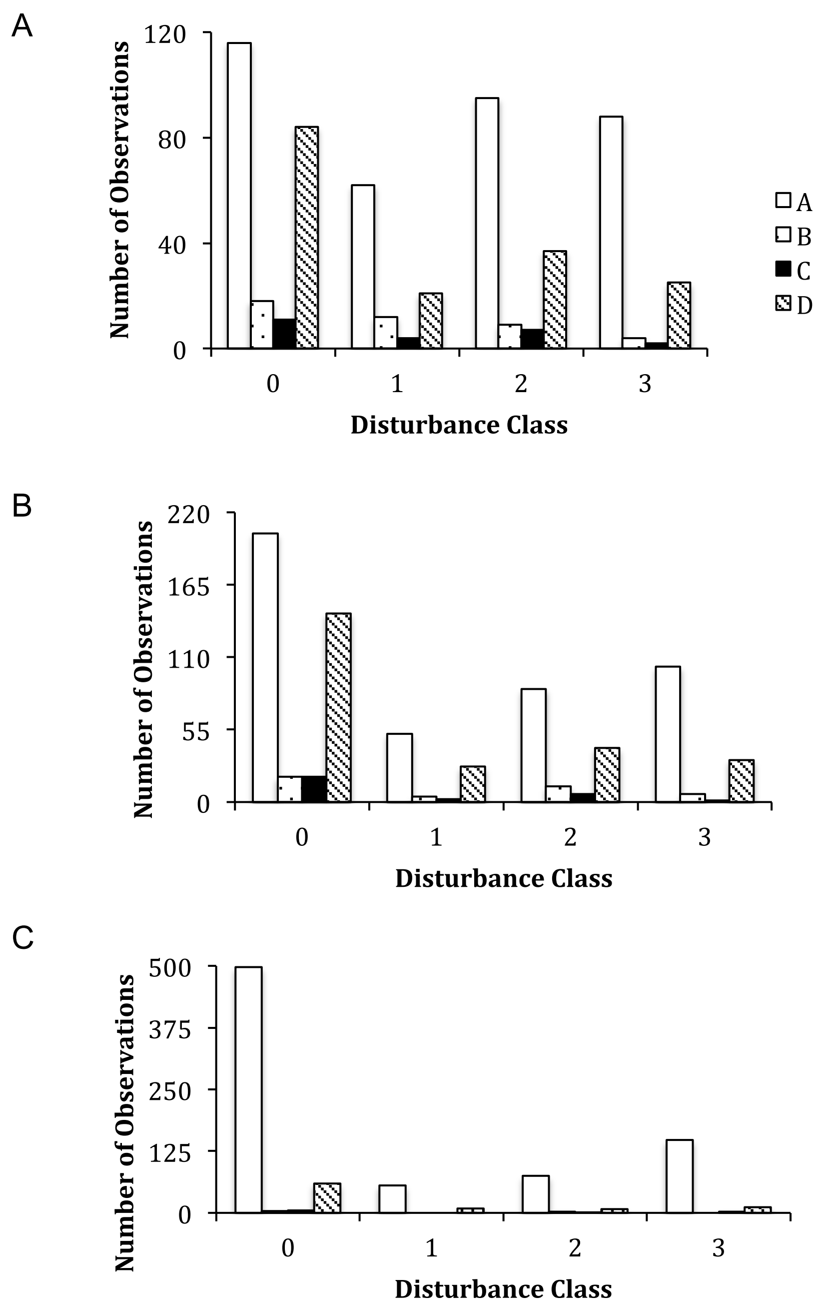


Figure 5. Number of observations of behaviour, from A to D, by disturbance class for the active season (A), mating season (B), and inactive season (C). "A" behaviour indicates a concealed behaviour, such as non-visible behaviour, whereas a "D" behaviour indicates a non-concealed behaviour, such as visible fully-coiled. A disturbance class of 0 indicates undisturbed, whereas a disturbance class of 3 indicates highly disturbed. Higher counts reflect a higher probability of that particular behaviour occurring at each particular disturbance level.
undisturbed areas.

During the inactive season, disturbance is not a significant predictor of behaviour ($p > 0.05$).

Probability of being visible

The best model for this analysis does not include an interaction between disturbance and season (Table IV). There was no need to conduct separate analyses by season. The best model shows that when snakes are in highly disturbed areas, they are significantly more likely to remain non-visible ($p < 0.0001$) (Fig. 6).

Table IV. Model selection (top panel) and details of the final model (bottom panel) for probability of visible behaviour of western diamond-backed rattlesnakes in areas of varying disturbance levels. *k* = the number of parameters in the model, AIC = Akaike's information criteria value, and ΔAIC = difference between AIC values for the best model (bolded) and each other model.

Model	**k**	**AIC**	**ΔAIC**
Random Effects Included For Models Below	*(1 + Sex + Season | Individual)*		
Probability of movement = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season + Disturbance : Sex : Season	22	2418.99	11.70
Probability of movement = Disturbance + Sex + Season + Disturbance : Sex + Disturbance : Season + Sex : Season	20	2416.38	9.09
Probability of movement = Disturbance + Sex + Season + Disturbance : Sex + Sex : Season	18	2413.31	6.02
Probability of movement = Disturbance + Sex + Season + Disturbance : Sex	16	2410.97	3.68
Probability of movement = Disturbance + Sex + Season	**15**	2409.25	**1.96**
Probability of movement = Disturbance + Season	**14**	**2407.29**	**0**
Coefficient	**Value (SE)**	**DF**	**p**
Intercept	-0.14 (0.13)	2235	0.292
Disturbance	-0.24 (0.05)	2235	<0.0001
Season (Inactive)	-1.94 (0.23)	2235	< 0.0001
Season (Mating)	-0.05 (0.13)	2235	0.678

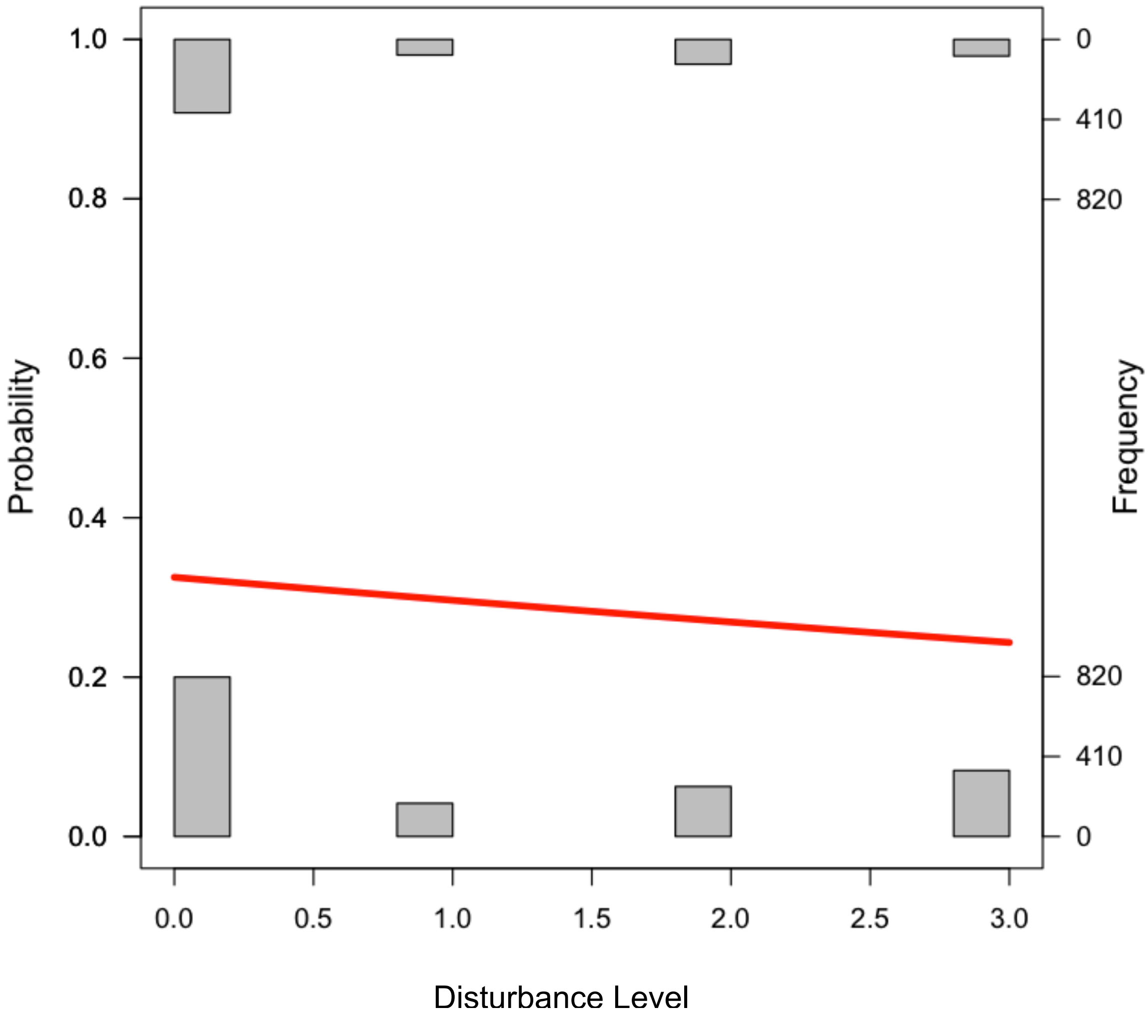


Figure 6. Frequency of observed data (histograms) and probability of western diamond-backed rattlesnake visible behaviour as disturbance increases (from Class 0 to Class 3) where 0 = non-visible behaviour, 1 = visible behaviour.

X. DISCUSSION

In our study, we attempted to model the relationship between anthropogenic disturbance and movement patterns of western diamond-backed rattlesnakes. Our results indicate that snakes are significantly affected by anthropogenic disturbance during the mating and active seasons. During these seasons, snakes in highly disturbed areas are significantly more likely to move. However, anthropogenic disturbance appears to have little effect in the inactive season on probability of movement. Further, disturbance has no significant effect on distances moved by western diamond-backed rattlesnakes, regardless of season. In our study, we also modeled the relationship between anthropogenic disturbance and behaviour patterns of western diamond-backed rattlesnakes. Results suggest that snakes are significantly more likely to remain concealed in highly disturbed areas and to remain unconcealed in undisturbed areas. Again, disturbance is not a significant predictor of behaviour during the inactive season. We also examined the relationship between anthropogenic disturbance and visibility behaviour. For this logistic regression analysis, there was no need to split up the analyses by season. Thus, regardless of season, snakes in highly disturbed areas are significantly more likely to remain non-visible.

The results of our study provide support for the hypothesis that anthropogenic disturbance has an effect on the movement patterns of western diamond-backed rattlesnakes. We predicted that snakes in highly disturbed areas would move significantly more than snakes in undisturbed areas. The findings are consistent with our prediction. Snakes in highly disturbed areas are significantly more likely to move than snakes in undisturbed areas, during the mating and active season. The mating season consists of two periods during the year; the first mating season is during the spring (approximately March 31 to May 25) and the second mating season is during the fall (approximately August 18 to October 19). The active season falls in the middle of these two mating seasons, from approximately May 26 to August 17. From the end of March to mid-October, the ambient temperatures are higher at the ASDM (Fig. 3). This may contribute to the snakes' ability to move more frequently during the mating and active seasons.

It is also important to consider how tourist visitation to the ASDM may impact probability of movement. As presented in Figure 7, the peak time for tourists at the ASDM is between February and April. The higher tourism rate during April coincides with the spring mating season. Thus, high tourism rates may contribute to the increased probability of movement during the mating seasons. During these periods of high human traffic, snakes likely experience a greater incidence of interactions with humans and choose to move locations frequently in order to avoid this contact. This explanation is likely, especially since Sealy (2002) also found evidence that a male timber rattlesnake actively avoided human-modified landscapes. However, tourist traffic at the ASDM is unable to explain the increased probability of movement during the active season. It is important to note, however, that this visitation data is only for one year and may not fully represent the tourist trends from 2005 to 2011. Another important point to note is that disturbance was not found to be a significant predictor of distances moved. These results suggest that disturbance impacts whether or not a snake will move in avoidance but disturbance does not impact how *far* the snake will move in avoidance.

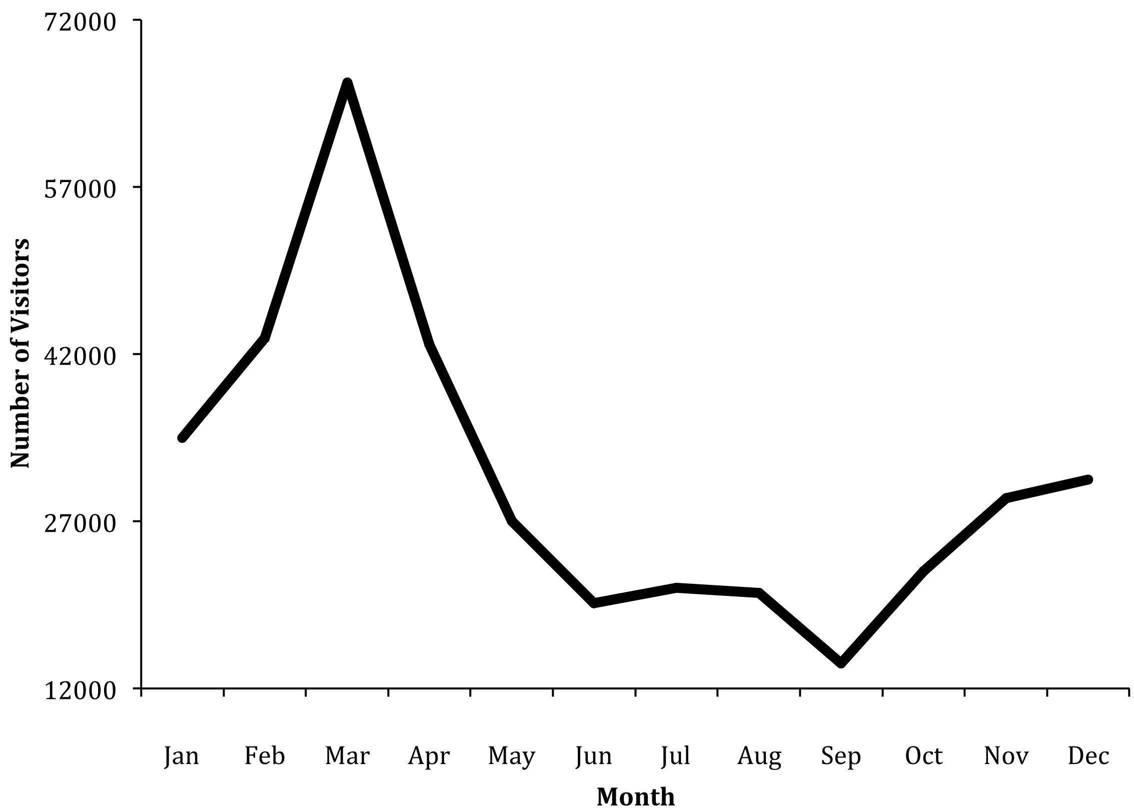


Figure 7. Number of visitors to the Arizona-Sonora Desert Museum, per month for year 2013.

The results of our study also provide support for the hypothesis that anthropogenic disturbance has an affect on the behaviour patterns of western diamond-backed rattlesnakes. We predicted that in highly disturbed areas, snakes would remain concealed, exhibiting more cryptic behaviour. Our findings are consistent with this prediction. Specifically, we found that during the mating and active seasons, snakes are significantly more likely to remain concealed in highly disturbed areas. Again, the ASDM receives most of its tourist traffic during the spring mating season. Thus, humans are more abundant on the museum grounds during the time, and human-snake interactions are more likely. With more humans present, snakes are more likely to behave cryptically, by remaining concealed, or visible and stretched. A stretched body position better allows the snake to escape an unfavourable situation, as compared to a fully-coiled body position. This higher tourist traffic during the spring may explain why snakes are more likely to remain concealed during the mating season. However, the peak season for tourists does not completely coincide with the active season. Temperature may be more important to consider in this case, as snakes are likely remain comfortably shaded and concealed during periods of high heat, such as during the active and fall mating seasons.

We also found that, regardless of season, snakes are more likely to remain non-visible in highly disturbed areas. The available literature supports our findings that anthropogenic disturbance affects behaviour patterns in animals (Ohashi *et al.* 2013, Ciuiti *et al.* 2012, Burger 1994). Specifically, Ciuiti *et al.* (2012) found that human disturbance, in the form of hunting activity, caused a significant increase in elk vigilance behaviour. Similarly, Burger (1994) found that in areas where there were more human visitors, piping plovers allotted significantly more time to vigilance behaviour and, subsequently, less time to foraging. Ohashi *et al.* (2013) found that wild boars increased nocturnal activity, when in closer proximity to hunting activity and human settlement. Our findings are consistent with the available literature, suggesting that anthropogenic disturbance can significantly alter behaviour patterns, which may lead to other negative side effects, such as reduced foraging.

The findings from our study can be applied to mitigate the effects of anthropogenic disturbance on western diamond-backed rattlesnakes. For example, subsequent to the results of Sealy's (2002) study, management practices at Hanging Rock State Park, North Carolina, were reviewed and one hiking trail was closed to reduce human traffic through a timber rattlesnake gestation site. Further, human-reptile interactions are not well studied and our study provides valuable insight into the consequences of these interactions. Although our study was not able to disentangle the separate effects of direct and indirect anthropogenic disturbance, the results of our study can help to govern how new conservation policy and management is created. Further, western diamond-backed rattlesnakes can be viewed as a model system to assist in our overall understanding of how anthropogenic disturbance affects wildlife. Already, the extinction of species globally is increasing due to habitat degradation, fragmentation, and destruction (Gibbons 2000). Not only are we, humans, reducing viable habitat necessary for wildlife species to thrive and survive, but our mere presence is generating direct and indirect anthropogenic pressures on nature (Rodriguez-Prieto & Fernandez-Juricic 2005). In summary, the findings from our study are important in understanding how human presence in nature has an impact on aspects of everyday animal life, such as movement and behaviour.

XI. REFERENCES

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2013). Lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5, http://CRAN.R-project.org/package=lme4

Beyer, H. L. (2004). Hawth's analysis tools for ArcGIS. Http://www. spatialecology.com/htools [accessed 10 February 2014].

Brown, G. W. (2001). The influence of habitat disturbance on reptiles in a Box-Ironbark eucalypt forestof south-eastern Australia. *Biodiversity and Conservation 10*, 161-176.

Burger, J. (1994). The effect of human disturbance on foraging behaviour and habitat use in piping plover (*Charadrius melodus*). *Estuarine Research Federation 17*(3), 695-701.

Carney, K. M., & Sydeman, W. J. A review of human disturbance effects on nesting colonial waterbirds. (1999). *Waterbirds: The International Journal of Waterbird Ecology 22*(1), 68-79.

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of human on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PlosOne 7*(3), 1-13.

Dobson, A. P., Rodriguez, J. P., Roberts, W. M., & Wilcove, D. S. (1997). Geographic distribution of endangered species in the United States. *Science* 275, 550-553.

Environmental Systems Research Institute (ESRI) Inc. (2013). v. 10.0, Redlands, California, USA.

Ficetola, G. F., Sacchi, R., Scali, S., Gentilli, A., De Bernadi, F., & Galeotti, P. (2007). Vertebrates respond differently to human disturbance: Implications for the use of a focal species approach. *Acta Oecologica* 3, 109-118.

Garland, T. Jr., & Adolph, S. C. (1994). Why not to do two-species comparative studies: Limitations on inferring adaptation. *Physiological Zoology 67*, 797–828.

Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., et al. (2000). The global decline of reptiles, déjà vu amphibians. *BioScience 50*(8), 653-666.

Glaudas, X. (2004). Do cottonmouths (Agkistrodon piscivorus) habituate to human confrontations? *Southeastern Naturalist 3*(1), 129-138.

Glaudas, X., Winne, C. T., & Fedewa, L.A. (2006). Ontogeny of anti-predator behavioural habituation in cottonmouths (Agkistrodon piscivorus). *Ethology,* 608-615.

Google Inc. (2013). v. 7.0.3.8542, Mountain View, California, USA.

Johnson, J., Ivanyi, C. S., & S. Poulin. 2002. Rattlesnake translocation at the Arizona-Sonora Desert Museum. Current Research on the Herpetofauna of the Sonoran Desert II, April 2003. (Poster)

Liley, D., & Sutherland, W. J. (2007). Predicting the population consequences of human disturbance for ringed plovers *Charadrius hiaticula*: A game theory approach. *The International Journal of Avian Science* 1, 82-94.

Nowak, E. M., Hare, T., & McNally, J. (2002). Management of "nuisance" vipers: effects of translocation on western diamond-backed rattlesnakes (Crotalus atrox) IN *Biology of the Vipers.* Schuett, G. W., Hoggren, M., Douglas, M. E., & Greene, H. W., editors. Eagle Mountain Publishing.

Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H., Kuwabara, T., Hiroshige, Y., Koike, S., Hoshino, Y., Toda, H., & Kaji, K. (2013). Differences in that activity pattern of the wild boar *Sus scrofa* related to human disturbance. *European Journal of Wildlife Research* 59, 167-77.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rodriguez-Prieto, I, & Fernandex-Juricic, E. (2005). Effects of direct human disturbance on the endemic Iberian frog *Rana iberica* at individual and population levels. *Biological Conservation* 123, 1-9.

Rodriguez-Prieto, I., Martin, J., & Fernandez-Juricic, E. (2010). Habituation to low-risk predators improves body condition in lizards. *Behavioural Ecology and Sociobiology* 64, 1937-1945.

Sala, O. E., Chapin III, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science* 287, 1770-1774.

Sealy, J. B. (2002). Ecology and behaviour of the timber rattlesnake (Crotalus horridus) in the upper piedmont of North Carolina: Identified threats and conservation recommendations IN *Biology of the Vipers.* Schuett, G. W., Hoggren, M., Douglas, M. E., & Greene, H. W., editors. Eagle Mountain Publishing.

Venables, W. N., & Ripley, B. D. (2002). Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN: 0-387-95457-0.

Weatherhead P. J., & Blouin-Demers, G. (2004). Long-term effects of radiotelemetry on black ratsnakes. *Wildlife Society Bulletin 32*, 900-906.

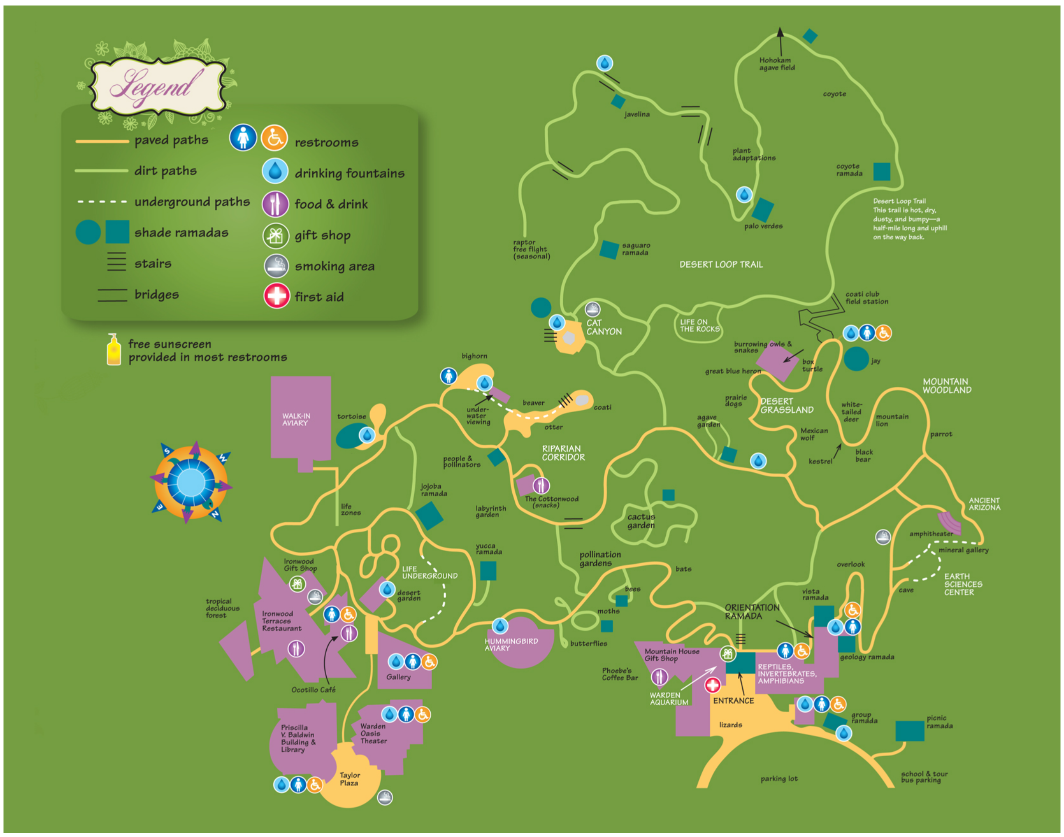
XII. APPENDIX

1.1 – Figure 1. Photograph of the mountainous desert scrub terrain present at the ASDM. Source: http://grandarizona.com/arizona65.jpg.

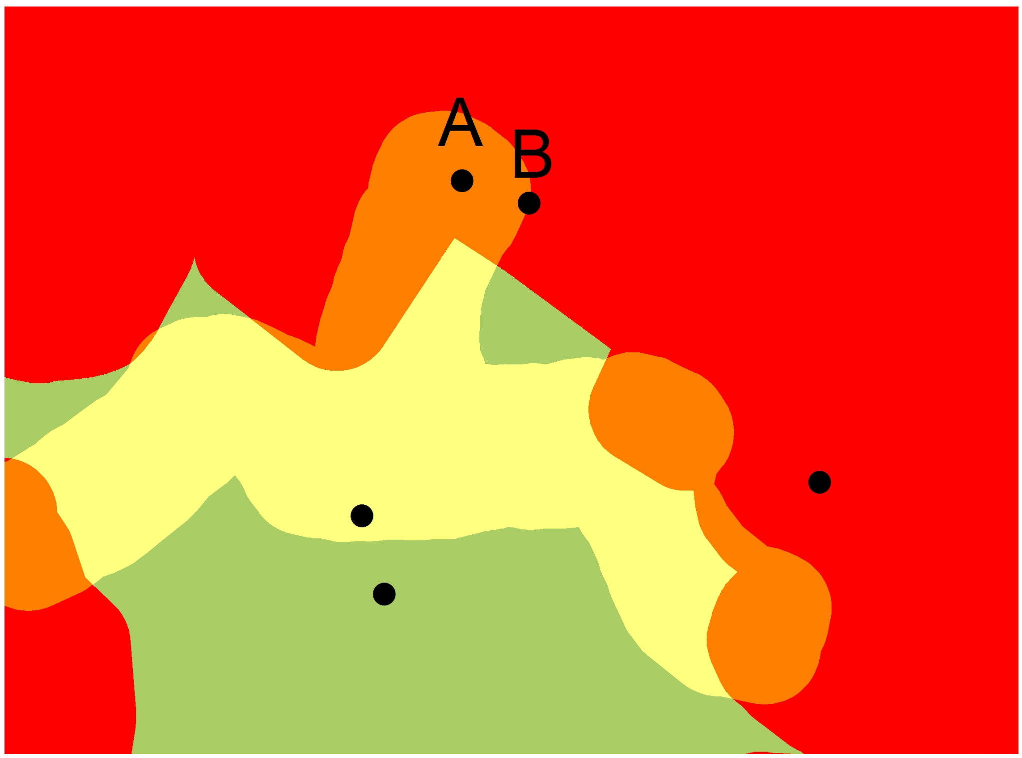
1.2 – Table I. Identification, mass, date captured, date transmitter removed, number of observations, and notes on recapture or death, per individual snake.

Snake ID	Mass (g)	Date of Implantation	Date Transmitter Removed	Number of Observations	Notes
A	680	7/3/2005	2/1/2006	45	RF
B	550	7/2/2005	10/6/2006	111	SF?
C	265	6/4/2005	9/16/2005	36	RF
D	505	6/30/2005	9/27/2006	120	RS
E	1155	6/8/2005	5/3/2006	97	SF?
F	740	7/25/2005	10/6/2005	23	RS
G	550	9/9/2005	7/25/2006	74	RS
H	300	9/20/2005	7/29/2010	263	AC
I	560	4/23/2006	8/28/2008	139	AC
J	605	5/12/2006	8/8/2007	113	SF?
K	335	5/12/2006	4/22/2008	141	AC
L	480	9/24/2006	3/16/2008	92	RF
M	855	10/12/2006	10/7/2008	100	RF
N	415	5/12/2007	9/17/2008	81	AC
O	665	6/21/2007	9/23/2008	68	RF
AA	365	3/28/2008	9/23/2008	30	SF
BB	355	4/10/2008	5/27/2008	12	RS
CC	370	7/3/2008	7/1/2010	117	AC
DD	310	9/18/2008	9/16/2010	132	AC
EE	355	4/17/2009	5/17/2011	122	AC
FF	465	5/14/2009	3/23/2011	108	AC
GG	440	9/9/2010	5/13/2012	92	SF?
HH	450	4/7/2011	5/23/2013	85	AC
JJ	410	5/6/2011	-	51	IN
KK	395	9/1/2011	5/9/2013	80	AC

A – Single letters indicate male
AA – Double letters indicate female
AC – animal captured and radiotransmitter was removed
RF – Radiotransmitter found without snake remains
SF – Snake found with transmitter (SF? – snake found and, presumably, transmitter found with it, not specified)
RS – Radiotransmitter found with all or some of snake remains
IN – Inactive radiotransmitter, snake presumably lost



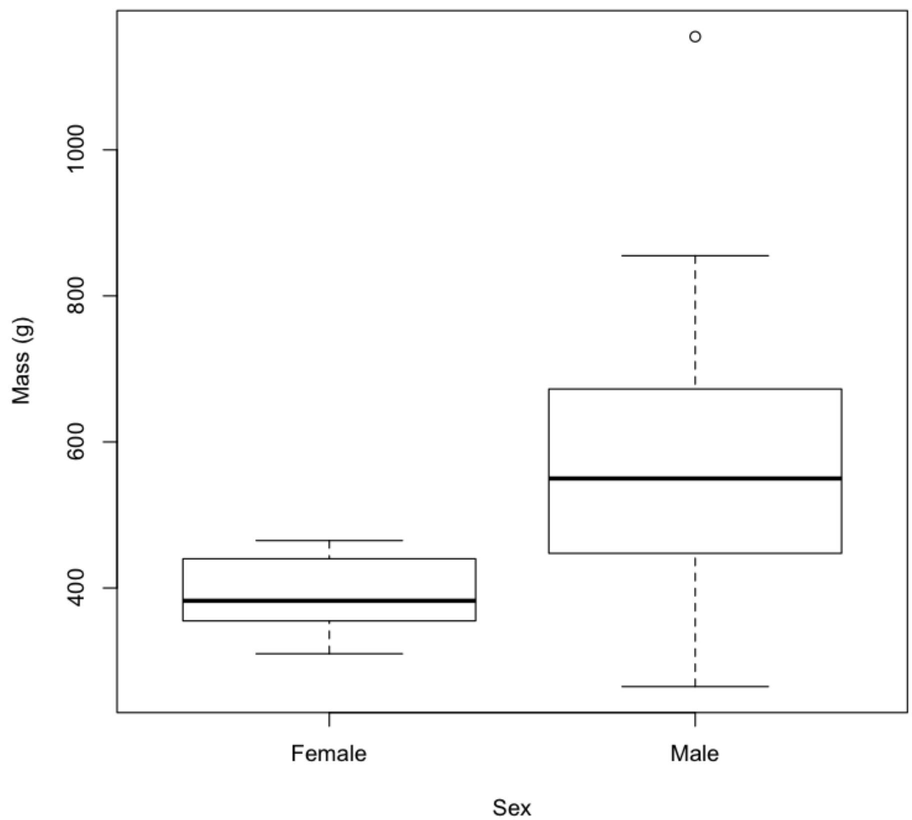
1.3 – Figure 2. Map of ASDM public grounds, used as cross-reference, to create disturbance polygons in *Google Earth*. Source: https://www.desertmuseum.org/images/ASDM _map_medium.jpg



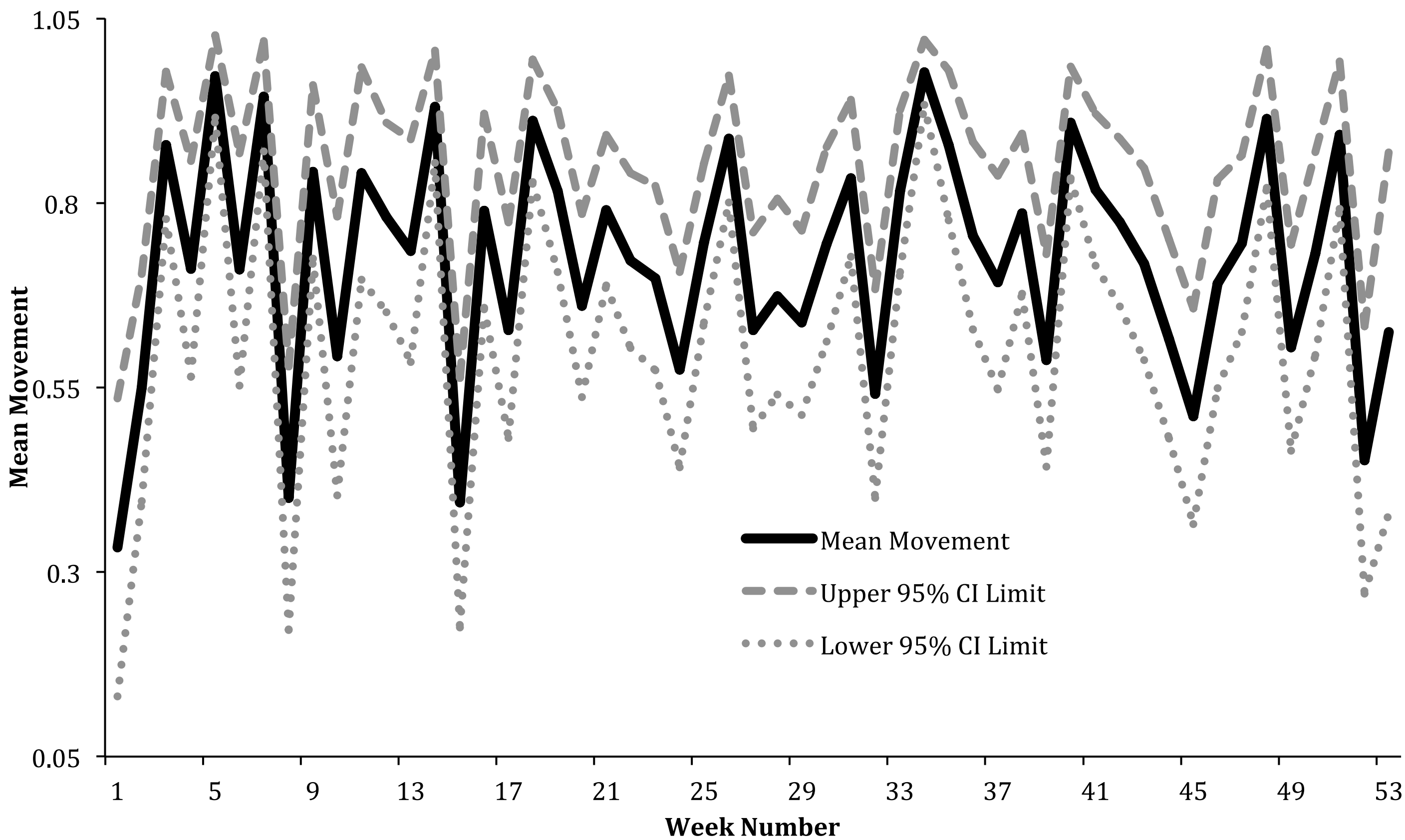
1.4 – Figure 3. Example of radiotelemetry locations that could receive either a Level 2 or Level 3 classification. Red represents the Level 3 disturbance layer and yellow represents the Level 2 disturbance layer. Orange represents where the Level 2 and Level 3 buffered layers intersect. Green represents the Level 1 disturbance layer. Radiotelemetry locations A and B both receive a Level 3 disturbance category, as discussed in *Methods.*

1.5 – Table II. Number of radiotelemetry locations classified under Disturbance Level 3, Level 2, Level 1, and Level 0, as determined by buffer distance applied.

Disturbance zone	2 meter buffer	5 meter buffer	10 meter buffer
Level 3	296	439	598
Level 2	309	410	618
Level 1	367	254	82
Level 0	1356	1230	1034



1.6 – Figure 4. Boxplot of mass (in grams) per sex, for western diamond-backed rattlesnakes used in this study. The boxplot indicates that mass differs between the sexes. Thus, sex was controlled for in the analyses, rather than mass, as mass is indicated by sex.



1.7 – Figure 5. Mean movement per week and 95% confidence intervals (CI). Mean movement was determined by averaging the movement binary variable, across all individual snakes, per week. No movement (distances of under 5 m moved) is represented by 0 and movement (distance of 5m and over moved) is represented by 1. The upper (grey dashed line) and lower (grey dotted line) 95% confidence intervals are presented. This graph tells me that the frequency of movement and week number are not related and thus, it may not be necessary to control for seasonality in the statistical analyses.

1.8 – Modelling Example – Probability of Movement vs. Disturbance Level

Temperature Model (df = 13, AIC = 2441.322):

movfreq ~ dist5+sex+temp+sex*temp+sex*dist5+dist5*temp+
(1+sex+temp|ind)

Season Model (df = 20, AIC = 2426.558):

movfreq ~ dist5+sex+season+sex*season+sex*dist5+dist5*season+
(1+sex+season|ind)

1.9 – Table III. Comparison of results from four statistical analyses for disturbance levels determined by two meter buffer zones, five meter buffer zones, and ten meter buffer zones.

Analysis and Parameters		**2 m buffer p-values**	**5 m buffer p-values**	**10 m buffer p-values**
Probability of movement vs. disturbance, logistic regression	Random effects	1+season|ind	1+season+sex|ind	1+season|ind
	Intercept	< 0.0001	< 0.0001	< 0.0001
	Dist	0.053	0.058	0.237
	SeasonI	< 0.0001	< 0.0001	< 0.0001
	SeasonM	0.047	0.011	0.024
	Dist*seasonI	0.017[a]	0.057	0.424
	Dist*seasonM	0.017[a]	0.001[a]	0.008[a]
Analysis and Parameters		**2 m buffer p-values**	**5 m buffer p-values**	**10 m buffer p-values**
Distance moved vs. disturbance, linear mixed effects model	Random effects	1+season|ind	1+season|ind	1+season|ind
	Intercept	< 0.0001	< 0.0001	< 0.0001
	Dist	NA	NA	0.037
	SeasonI	< 0.0001	< 0.0001	< 0.0001
	SeasonM	0.044	0.044	0.037
Analysis and Parameters		**2 m buffer p-values**	**5 m buffer p-values**	**10 m buffer p-values**
Behaviour vs. disturbance, ordinal logistic regression	Dist	< 0.0001	< 0.0001	< 0.0001
	SeasonI	< 0.0001	< 0.0001	< 0.0001
	SeasonM	0.601	0.596	0.482
	Dist*seasonI	0.005[a]	0.015[a]	0.027[a]
	Dist*seasonM	0.311	0.352	0.254
Analysis and Parameters		**2 m buffer p-values**	**5 m buffer p-values**	**10 m buffer p-values**
Visibility behaviour vs. disturbance, logistic regression	Random effects	1+season+sex|ind	1+season+sex|ind	1+season|ind
	Intercept	0.372	0.292	0.680
	Dist	< 0.0001	< 0.0001	< 0.0001
	SeasonI	< 0.0001	< 0.0001	< 0.0001
	SeasonM	0.418	0.678	0.704
	Dist*seasonI	0.012[a]	NA	NA
	Dist*seasonM	0.391	NA	NA

b - for a significant p-value for the dist*season parameter, refer to Table 3 for further comparison of statistical results (separated by season)

1.10 – Table IV. Further comparison of statistical results, separated by three seasons, for disturbance determined by two meter buffer zones, five meter buffer zones, and ten meter buffer zones.

Analysis	Season	2 m buffer p-values	5 m buffer p-values	10 m buffer p-values
Probability of movement vs. disturbance, logistic regression [a]	Mating	0.208	0.03	0.007
	Active	0.033	0.042	0.158
	Inactive	0.185	0.295	0.735
	Season	**2 m buffer p-values**	**5 m buffer p-values**	**10 m buffer p-values**
Behaviour vs. disturbance, ordinal logistic regression	Mating	0.002	0.002	0.005
	Active	< 0.0001	< 0.0001	< 0.0001
	Inactive	0.528	0.161	0.102
	Season	**2 m buffer p-values**[b]	**5 m buffer p-values**	**10 m buffer p-values**
Visibility behaviour vs. disturbance, logistic regression	Mating	0.004	NA	NA
	Active	< 0.0001	NA	NA
	Inactive	0.343	NA	NA

a - all three buffer analyses had |ind as random effect
b - two meter buffer analysis had |ind as random effect