University of Arkansas, Fayetteville ScholarWorks@UARK

Graduate Theses and Dissertations

5-2023

Factors That Affect Home Range of Timber Rattlesnakes (Crotalus horridus) in Northwest Arkansas

Bannon Gallaher University of Arkansas-Fayetteville

Follow this and additional works at: https://scholarworks.uark.edu/etd

Part of the Animal Experimentation and Research Commons, Animal Studies Commons, Behavior and Ethology Commons, Terrestrial and Aquatic Ecology Commons, and the Zoology Commons

Citation

Gallaher, B. (2023). Factors That Affect Home Range of Timber Rattlesnakes (Crotalus horridus) in Northwest Arkansas. *Graduate Theses and Dissertations* Retrieved from https://scholarworks.uark.edu/etd/5073

This Thesis is brought to you for free and open access by ScholarWorks@UARK. It has been accepted for inclusion in Graduate Theses and Dissertations by an authorized administrator of ScholarWorks@UARK. For more information, please contact scholar@uark.edu.

Factors That Affect Home Range of Timber Rattlesnakes (*Crotalus horridus*) in Northwest Arkansas

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology

by

Bannon Gallaher University of Arkansas Bachelor of Arts in Biology, 2014

May 2023 University of Arkansas

This thesis is approved for recommendation to the Graduate Council.

Steven J. Beaupre, Ph.D. Thesis Director

Michael E. Douglas, Ph.D. Committee Member

Jason Tullis, Ph.D. Committee Member

Abstract

Conservation of animal populations requires knowledge of their habitat and spatial needs. Quantifying spatial requirements involves the analysis of home range. We examined the effects of sex, body size (SVL), body condition (log mass/log SVL), and year on home range in Timber Rattlesnakes (Crotalus horridus) in Northwest Arkansas. Individual locality data from an ongoing, 22+ year radio-telemetry study in Madison Co., Arkansas were analyzed using both minimum convex polygon (MCP) and Kernel Density Estimates (KDE). Plots of the number of sequential observations versus home range (MCP and KDE) determined that a minimum of 25 locations per individual per active season (using weekly to bi-weekly sampling) were sufficient to generate a stable home range estimate using MCP and KDE methods. Restriction to samples of \geq 25, resulted in 120 snake-years of data, distributed among 54 individuals (25 males and 29 females). Home ranges were estimated using ArcGIS 10.4 with HRT extension. Mixed model ANCOVA revealed a significant SVL by Sex interaction. Male MCP increased with body size, whereas, no effect of body size was detected for females. Improved body condition (log mass/log SVL) increased MCP and KDE (90% and 95%) in males, but not in females. Home range was compared within individuals among years (MANOVA). Significant annual differences in home range centroid were observed in 21 of 23 individuals with a minimum of three years of data. Our results verify that spatial needs of males and females differ, and importantly, suggest that home range frequently shifts in location among years. We support the notion that habitat use of C. horridus is highly variable and requires large sample size across seasonal and annual temporal scales to best inform conservation activities.

Acknowledgments

I thank the University of Arkansas, Ozark Natural Science Center, the Arkansas Natural Heritage Commission, and the Arkansas Game and Fish Commission for allowing our work to take place on their property. I want to thank my amazing parents and sister for supporting me in many ways but especially my academics. My parents made the outdoors a part of my life from such a very young age and to them I owe my fascination and stewardship of nature. Next, I would like to thank my "Science Dad", Steve Beaupre, and the rest of my snake family, Jason Ortega, Craig Lind, Larry Kamees, Brenna Levine, Casey Brewster, Max Carnes-Mason, Allie Litmer and all that have come before me. I have never experienced a more genuine and caring group of people. It has been an honor to be a part of the "island of misfit toys" with all of you. I'd like to thank Mike Douglas for all the pep talks, guidance, and wisdom. To all of my friends that pretended to listen to me talk about my research and question why I have not graduated yet, thank you as well. Lastly, I would be remiss to not acknowledge my many students both at the University of Arkansas and at The New School. My students deserve a medal for listening to rattlesnake rants but as I have learned from others, and you have learned from me, my highest hope is that you continue the legacy of learning.

Table of Contents

Introduction
The Importance of Home Range Studies to Conservation1
Distribution of Resources1
Technology2
Home Range Analysis
Materials and Methods
Study Site9
Study organisms
Radiotelemetry
Home Range11
Effect of Sample Size on Stability of Home Range12
General Statistical Approach12
Sex
Body Size
Annual Variation
Results
Sample Size Effect on Stability of Home Range
Sex and Body Size
Body condition
Annual Variation
Discussion
Observation Requirements
Sex
Body Size
Body Condition
Annual variation
References

Introduction

The Importance of Home Range Studies to Conservation

Understanding the spatial ecology of a population can aid in determining and delivering the most appropriate and feasible management plans. Home range (HR) studies inform management and conservation strategies deployed for species of concern (Adams, 2005; Carfagno & Weatherhead, 2008; MacGowan & Walker, 2013). Estimates of HR using various techniques can further elucidate habitat requirements for animal-centric management. Requirements deduced from HR studies include the estimated area an individual uses in a given season, land cover types (forest, glade, wetlands, etc.), and measures of distance traveled (Petersen et al., 2019; Waldron et al., 2006). Studies using HR methods can also illustrate the vulnerability to habitat fragmentation and the likelihood of a species of concern recolonizing an extirpated site naturally (Webb & Shine, 1997).

Distribution of Resources

Landscape heterogeneity and the distribution of resources are known or suspected to affect animal home ranges (Duvall et al., 1992a). Resources such as food, water, mates, hibernacula, and refugia are rarely distributed across a landscape at random (Forman & Godron, 1981). Configurations of animal HR are expected to be distributed in clusters in proximity to resources relevant to their seasonal or life stage requirements (Burt, 1943). Movement patterns specific to a species biology such as migration (Cagle, 1944; Hundertmark, 1998; Schofield et al., 2010), territory defense (Jordan et al., 2007), hibernation (Brito, 2003; Brown et al., 1982), predator avoidance (Durant, 2000b, 2000a), and mate searching (Brown & Weatherhead, 1999; Lind & Beaupre, 2015) are also capable of affecting patterns in animal HR.

Technology

Technologies used to track individual animal locations have undergone great advancements since HR was defined by Burt in 1943. The use of very high frequency (VHF) radio devices to track wildlife began in the 1960s (Cochran & Lord, 1963). Very high frequency transmitters attached to animals emit electromagnetic pulses at set frequencies that would then be detected using a directional antenna connected to a receiver (Bridge et al., 2011). Radio telemetry allowed investigators to determine the animal's location by closing the distance between the transmitter and antenna (vehicle mounted or handheld). Transmitters have improved in their signal range, battery life, and size, thus allowing application to smaller species, even insects (Bridge et al., 2011). After civilians were given access to global positioning systems (GPS) in 2000, wildlife with fixed transmitters could be tracked from distances all over the world (Kaczensky et al., 2010). Satellite telemetry provides location fixes through signals transmitted from satellites in a known orbit. Signals communicate the position of the satellite and the time the signal was sent. Surface GPS devices receive the signals transmitted from a minimum of four satellites to generate an explicit location. The GPS device calculates the distance separating the satellite from the device based on signal transit time and exact location of the satellite (Beaupre, 2016). When GPS was first introduced to wildlife tracking in 1994, the estimated positional error (EPE) was >150m (Argos, 1996). Now, GPS instruments allow investigators to consistently obtain locations <10m of EPE (our equipment; Garmin III handheld GPS and newer). Biotelemetric studies of animal behavior have enjoyed increased impact as location technologies become more accurate and sensitive. Location, however, is not the only biologically relevant data to be collected. In our C. horridus population, using radiotelemetric tracking by foot allows investigators to collect additional data such as body temperature (per temperature sensitive

2

transmitters), body posture and behavioral activity (foraging, mating, resting, thermoregulation, digestion, etc.), habitat type and structure, association with unmarked Timber Rattlesnakes, ecdysis and general observations of the animal appearance (fungal infections caused by overwintering sores, wounds from predation, or mortality events; (Beaupre, 2008; Gardner-Santana & Beaupre, 2009; Lind & Beaupre, 2015; Wills & Beaupre, 2000).

Limitations to GPS technologies such as hardware size, battery life, and signal strength established via an external antenna prevent researchers from surgically embedding devices that allow for more frequent collection of location data. Specifically, external antennas required to receive satellite signals pose risks by obstructing movement by catching on environmental obstacles, discomfort caused by passage of the device through the body wall, and prolonged exposure to potential infection (Beaupre, 2016). As a result, many investigators must continue to rely on radio telemetry to track and collect GPS location data.

Home Range Analysis

Home range analysis has experienced many improvements since 1943. Early quantification of area use by an individual was measured via minimum convex polygons (MCP) (Blair, 1940; Odum & Kuenzler, 1955). Kernel methods then addressed some of the short-comings of the MCP method by describing an animal's HR using a relative frequency distribution of locations (Worton, 1989). In doing so, the kernel density estimation method can illustrate various levels of likelihood that an animal would occupy any point in space at any given time (Kie et al., 2010). Most common among kernel density estimation literature is the use of core activity areas, 50% (Samuel et al., 1985) and 95% isopleths that depict the total area used with 5% removed to account for occasional sallies that are typically described as exploratory in nature, respectively (Powell, 2000).

A frequent concern in the analysis of animal movement is the potential presence of autocorrelation (Hansteen et al., 1997). Autocorrelation occurs when the measurement of variables such as temperature, velocity, acceleration or in our case, position, at one point in time are statistically correlated with measures taken at another point in time. As measurements or sampling of variables are more temporally or spatially distant from one another the information becomes less redundant (Fleming et al., 2015; Swihart & Slade, 1985a). Autocorrelation is a consequence of the continuous process of animal movement and can persist across temporal scales that extend from hours or days to months or years (Fleming et al., 2015). We herein acknowledge the potential adverse effects of autocorrelation in HR estimation methods. However, due to our temporally dispersed sampling regimen to collect location data throughout the active season we are confident that any autocorrelation effects on our results are mitigated (Swihart & Slade, 1985a).

Animal movement patterns and HR can be shaped by variation in landscape, body size, and habitat productivity (Carfagno & Weatherhead, 2008). Animal movement patterns can be influenced by inaccessible terrain, habitat preference or avoidance (Kapfer et al., 2010), environmental destruction, habitat degradation and fragmentation (Loehle & Li, 1996; Tilman et al., 1994), thermal constraints (Huey, 1982), predator avoidance, and competition (interspecific and intraspecific) among others.

Home range is conceptual in nature and has two components: familiarity and use. The "use" component refers to the propensity of animals to in some way utilize spatiotemporal resources (Burt, 1943). Familiarity with an area is maintained through exploratory sallies without the need to physically return to those previous locations (Hayne, 1949; Powell, 2000). Animals experience familiarity in a gradient-like fashion which makes quantification difficult for investigators (Powell, 2000). To do so a more operational definition of HR required components that quantify use and estimate some degree of familiarity. One such method was first introduced by Hayne (1949) is the minimum convex polygon (MCP). Minimum convex polygon method is a smallest polygon drawn that includes all animal location data (Hayne, 1949). Using the area of the polygon, the HR area can then be quantified. The MCP method assumes that animals are using and familiar with 100% of the habitat that surrounds their movements within the boundaries of the polygon which often leads to an overestimation (Reed & Douglas, 2002; Row & Blouin-Demers, 2006; Wastell & Mackessy, 2011). A drawback of the MCP method is that often, animals will make sallies away from areas they are familiar with (Powell, 2000). In some cases, sallies can drastically increase the area of the MCP by including habitat that the animal has not accessed. However, such exploratory movements may still have biological function (e.g., mate search) and need to be considered by investigators. Sallies away from the core areas provide information and added familiarity to the animal's cognitive map. An increase in familiarity of the surrounding areas may enhance the animal's ability to utilize peripheries during

5

fluctuations in available resources (Powell, 2000) or during functionally dedicated episodic activities (King & Duvall, 1990).

One method that reduces the influence of sallies on HR area quantification is the kernel density estimation (KDE) method. Kernel density estimation uses nonparametric statistics to estimate the probability that an animal can be located in a given area based on the amount of time spent at any location (Silverman, 2003; Worton, 1989). Choosing to use KDE to estimate HR of animals requires selecting the width of the kernel also referred to in literature as "band width," or "smoothing parameter" (Seaman & Powell, 1996). Selecting a kernel width that is narrow will allow the nearest-neighbor observations to have the greatest influence on the density estimate. Whereas a wide kernel band width will allow neighboring observations from a further distance to influence the density estimate (Seaman & Powell, 1996; Silverman, 2003). Narrow bandwidths provide a fine-scale representation of the data whereas wide bandwidths are coarser and reveal less detail. Band width selection that is constant for the data (fixed kernel) or a band width that is varied (adaptive kernel) will provide varying results (Powell, 2000). Band width selection is a critical step when using the KDE method and should be based upon characteristics of the data being analyzed. Animal locations rarely resemble a bivariate, normal distributions (Horner & Powell, 1990; Seaman & Powell, 1996). The most appropriate band width selection procedure for distributions that are not normal is the least squares cross validation, LCSV (Powell, 2000). Least square cross validation selects a data-based bandwidth that has the smallest estimated error (Seaman & Powell, 1996; Silverman, 2003). Methods for estimating an animal's home range should be decided based on a case by case basis. There is no universal method that can be

developed for all animals. Seaman and Powell (1996) found that fixed kernels using the LSCV band width gave area estimates with little bias when analyzing simulated animal locations.

When designing appropriately scaled management strategies for the conservation of a species, spatial ecology studies provide managers with critical information such as preferred habitat type, quantified area requirements, movement patterns, and rates of movement. With the improvements to technologies such as GPS and VHF radio transmitters, researchers can investigate the spatial ecology of cryptic species such as snakes with lower monetary cost and tracking efforts. Timber rattlesnakes' large body size and slow pace of movement allows surgical implantation of radio transmitters that are capable of emitting high strength signals with multi-year battery life and track-ability by foot, respectively, and support Timber Rattlesnakes as model organisms for radio telemetry studies (Beaupre & Duvall, 1998). Additionally, interests in furthering the understanding of HR is shared by a large group of organisms, thus further supporting rattlesnakes as model organisms for studies of HR (Beaupre & Duvall, 1998).

Many conservation-centric studies have investigated key factors that drive snake movements. Hibernacula selection serves as a potential key factor in snake movement (Duvall et al., 1992a). Conditions of *C. horridus* dens (Agugliaro, 2011), presence of quality transitional hibernaculum (unencroached rocky outcroppings and leaf litter) as described by Adams (2005), GIS-based hibernacula modeling (Browning et al., 2005), and the absence of anthropogenic disturbances described by Reinert and Zappalorti (1988) have all improved the understanding of den usage by Timber Rattlesnakes. In iteroparous species such as *C. atrox*, den selection may be driven by participation in spring reproductive activity seen in communal den sites (Clark et al., 2014). Testosterone as described by Lind and Beaupre (2015) is a key factor in regulating male participation in mate-searching behaviors. During late summer and early fall, adult male *C. horridus* with adequate stored energetic capital increased participation in mate-searching movements while decreasing time spent in sit and wait ambush foraging postures (Lind & Beaupre, 2015). Gravid *C. viridis* as seen in Graves and Duvall (1993) executed lengthy but direct movements to commonly used rookery sites where individuals reduced activity to only include thermoregulatory egress and ingress from under rocks until parturition and neonatal first shed (Greene et al., 2002). Additionally, accessing critical resources among varying habitat types (Prey, refugia, mates ;Graves & Duvall, 1993; Hoss et al., 2010; Hyslop et al., 2014; Miller et al., 2012; Moore & Gillingham, 2006) and occasional exploratory sallies (Powell, 2000) influence seasonal snake movement patterns. Male individuals with heavier body mass as reported by Peterson (2019) had larger activity ranges compared to lesser mass males with no effect of body mass detected in females.

Studies of home range have been utilized and with a wide variety of snake species. Many studies use MCP methodologies for the simplicity and the ability to draw comparisons to less contemporary studies. Kernel density is also heavily utilized in the literature of spatial ecology involving snakes but lacks unified support due to inconsistency in KDE estimation of simulated and non-simulated studies, arguments of poor performance for highly autocorrelated data, inconsistent use of smoothing parameters, and controversial interpretation of biological relevance (Row & Blouin-Demers, 2006). Snake HR literature is dominated by studies that rely on few individuals, n < 20 (Adams, 2005; Beck, 1995; Danna L. Baxley & Carl P. Qualls, 2009; Hoss et al., 2010; Miller et al., 2012; Moore & Gillingham, 2006) and/or use short temporal scales, < 5 years. (Adams, 2005; Beck, 1995; Brito, 2003; Danna L. Baxley & Carl P. Qualls, 2009; Hoss et al., 2010; Hyslop et al., 2014; Miller et al., 2012; Moore & Gillingham, 2006). Resource distribution is expected to be patchily arranged across a landscape (Hoss et al., 2010; MacArthur & Pianka, 1966). Through time resource patches will change in their quality and location within the habitat (Baxley & Qualls, 2009). Animals will adapt their movement patterns seasonally and annually to encounter resources as needed (Baxley & Qualls, 2009; Gardiner et al., 2013; Kapfer et al., 2010). Some snake species can be relatively long lived (+20 years) and may experience changes in HR that are not captured if only studied for 1-2 years. Herein we present HR data from a long-term study of C. horridus in the Ozark Mountains of Northwest Arkansas. Specifically, we investigated the following questions: does sex, body size, and body condition of adult Timber Rattlesnakes affect the size of an individual's annual HR? Do individuals experience significant variation from yearto-year in their HR center?

Materials and Methods

Study Site

Our study was conducted on 6,070 hectares of contiguous habitat located in the Ozark Highland ecoregion of the Ozark Mountains owned and managed by the Ozark Natural Science Center (ONSC), Madison County Wildlife Management Area (MCWMA), and Bear Hollow Natural Area (Arkansas Heritage Commission) in Madison County, northwest Arkansas. Elevation ranged from 323 to 511m with a temperate annual climate, open and cedar-encroached cherty limestone glades, dolomite outcroppings, oak-hickory forests, ground water fed seasonally

intermittent streams, and food plots managed by Arkansas Game and Fish Commission (Barbour & Billings, 2000; Beaupre, 2008; Browning et al., 2005; Dyer, 2006).

Study organisms

We conducted our study on Timber Rattlesnakes (Crotalus horridus), a common and endemic pit viper in the Eastern United States, including the Ozark Mountain region. Snakes used throughout this study were captured opportunistically using visual surveys with highest efforts deployed during egress, ingress, or mating season. Snakes were captured (via tongs) opportunistically and a location was collected using GPS (Garmin GPS III, ±10m estimated positional error). Captured animals were transported using 10 gallon buckets with secure locking, aerated lids. Snakes were transported directly to the laboratory for morphometric measures and processing. Mass was measured $(\pm 0.01g)$ on a Sartorius model BP3100S digital scale and snout-vent length (SVL) was measured using a squeeze box (± 0.5 cm or $\pm 1\%$ of SVL; Beaupre, 2008; Quinn & Jones, 1974). Snakes were also permanently marked by injection of a PIT tag (passive integrated transponder, Avid Identification Systems, Inc., Norco, California). The transponder was intraperitoneally injected in the posterior segment of the body cavity, anterior to the tail. Snakes of sufficient size and sex distribution were retained for radio transmitter implantation. When processing was complete snakes were released at their point of capture.

Radiotelemetry

Captured snakes from 2000-2013 that met the size requirement determined by ASIH guidelines (2004; transmitters cannot exceed %5 of body mass, snakes >300g) received temperature sensitive radio transmitters (model SI-2T, Holohil Systems Ltd. Carp, Ontario, Canada) (Beaupre, 2008; Hardy Sr & Greene, 1999; Reinert & Cundall, 1982). During active season, April-November, (Lind & Beaupre, 2015), snakes were tracked two to three times per week using a Com-Spec R1000 (Communication Specialists, Norco, CA.) receiver in tandem with a hand-held Yagi 3-element directional antenna. As individuals were relocated, habitat use data were collected in addition to date, time, GPS coordinate (NAD 27, UTM), and estimated positional error (EPE). GPS devices used were Garmin III handheld units and only points with location accuracy of <10m EPE were included in HR analysis.

Home Range

Home Range was estimated using 100% MCP (Adams, 2005; Durbian et al., 2008) as well as kernel utilization distributions of 95%, 90%, and 50% (Seaman et al., 1999; Worton, 1989). Minimum convex polygon home ranges were created using ArcGIS 10.4.1. Home Range Tool (HRT 2.0; Rodgers, 2001) was used as an extension of ArcGIS 10.4.1 to calculate KDE (95%, 90%, 50%) with a least-square cross validation (LSCV) smoothing parameter, *h* (Row & Blouin-Demers, 2006). Least-square cross validation method is widely used and generally accepted as the most accurate of the available methods for data-based bandwidth estimation (Row & Blouin-Demers, 2006; Stevens & Barry, 2002).

Effect of Sample Size on Stability of Home Range

To assess the number of locations required to appropriately generate a home range estimation using the 100% MCP method we selected 10 males and 10 females with the greatest number of location points spread across active seasons (mean= 40.42, stdev= 4.40, range= 34-51). We then randomly sampled location points from individual annual data at increments of 10, 20, 25, 30, and 35. Randomly sampled points were then used to calculate MCPs at their respective increments. Home range size was plotted against number of observations (*n*) and visually inspected for an asymptote effect(Petersen et al., 2019; Row & Blouin-Demers, 2006).

General Statistical Approach

Data were analyzed with Program R statistical software (RStudio v3.5.0; R Core Team 2018). We analyzed data from 54 individuals (25males; 29 females) using parametric tests. Snake location data were collected from 2000-2014 with individual data ranging from a single complete year to seven years, both sequential and nonsequential. The variables we selected to examine in our home range analysis were sex (male and non-gravid female), SVL, and body condition index (BCI). Body condition was estimated using an index derived from *logwt / logSVL* (Beaupre, 2008; Lind & Beaupre, 2015).

The body condition index (BCI) values were integrated into a mixed model regression as the independent variable along with seasonal home range ha. (100% MCP, 95/90/50% KDE) and individual as the response variable and random factor, respectively. The effect of SVL on the relationship between sex and home range size was examined using an ANCOVA (Sokal &

Rohlf, 1981). Repeated measure mixed models were used to analyze the annual effects of sex, SVL, and BCI independently amongst individuals with multi-year data while accounting for individual as a random factor (Sokal & Rohlf, 1981). Residuals from models with predictor variables of sex, SVL, and BCI were inspected using Shapiro-Wilk to assess normality. Where warranted, log, square root, and squared transformations were assessed for best fit. To address the question of whether home ranges are stable from year-to-year we used a MANOVA to compare positional centroids among years. All data analyses were executed using an alpha level of 0.05.

Sex

We used a mixed model ANCOVA to determine the effect of sex (male or female; gravid females were excluded from this study due to low sample size) on home range size estimated with 100% MCP and KDE (95/90/50%) methods. We selected home range size as the response variable, length (SVL) and Sex as covariate and independent variables respectively, and individual as our random factor.

Body Size

The effect of body size (SVL) on MCP and KDE (95/90/50%) home range size was explored by fitting our data to a mixed model regression. Observations were separated into males and non-gravid females and analyzed separately due to failed mixed model slope heterogeneity test. The mixed model regression set HR size (ha.) as the response variable, SVL as the fixed effect, and individual as a random factor.

Annual Variation

We tested for variation among years in home range position using a MANOVA approach. Northing and easting coordinates were set as the response variables and year as a predictor variable. Data were selected from individuals who had a minimum of three tracking years (sequential and non-sequential). Twenty-four (8 males, 16 females) of the 55 total individuals were tracked for a minimum of three years (Range: 3 to 7 years). A MANOVA was conducted on the easting and northing data for each individual, comparing centroids among years. A total of 24 independent tests were conducted. To control overall experiment-wise type I error to 0.05, we used the Dunn-Sidak correction (Sokal & Rohlf, 1981). The correction estimates α ' which is the cutoff probability for each of k individual comparisons resulting in a total experiment-wise Type I error of $\alpha = 0.05$. The Dunn-Sidak error correction is given by $\alpha' = 1 - (1 - 0.05)1/k$. For k = 24 independent individual annual comparisons, the relevant cutoff value for each comparison is $\alpha' = 0.00214$. Thus, for all annual comparisons, the null hypothesis of no difference among years is rejected if p < 0.00214. The Dunn-Sidak correction is a conservative procedure with low power if more than one null hypothesis is rejected (Sokal & Rohlf, 1981), and therefore is likely to underestimate true differences among years.

Results

Our analysis of 120 snake years of data distributed amongst 54 individuals (26 males and 30 females) resulted in HR means for males of 25.77 (3.70 SE) ha. MCP, 45.66(7.05 SE) ha. KDE 95%, 36.15 (5.65 SE) ha. KDE 90%, 10.98 (1.89 SE) ha. KDE 50% and for females of 9.41 (1.59 SE) ha. MCP, 13.77 (1.56 SE) ha. KDE 95%, 10.94 (1.24 SE) ha. KDE 90%, 2.76 (0.37 SE) ha. KDE 50%. The SVL mean for males was 91.94cm (1.67 SE) and for females was

81.01cm (0.72 SE). The average mass for males was 754.78g (59.91 SE) and for females was 427.02g (13.46 SE).

Table 1 – Home range means (ha.) and dispersion statistics (standard deviation) for male and female *C. horridus* (N is number of individuals, s-y is number of snake-years represented).

Sex (N, s-y)	MCP (SE)	KDE95% (SE)	KDE90% (SE)	KDE50% (SE)
Male (25, 42)	25.77 (3.69)	45.56 (7.04)	36.15 (5.64)	10.96 (1.89)
Female (29, 77)	9.4 (1.5)	12.2 (1.55)	9.66 (1.23)	2.75 (0.36)

Sample Size Effect on Stability of Home Range

The plotted results from randomly sampled individual locations show that annual HR area calculated using MCP methodologies experiences an asymptote for rattlesnakes between 25 and 30 sampled locations; supporting our determination of minimum requirement of locations (n=25) for individuals to qualify for inclusion of this study.



MCP size by # of random sample observations

of random samples

Figure 1 – Line graph depicting minimum convex polygon (MCP) home range and number of randomly sampled location points from a single season. Male and female estimates are denoted by blue and red lines respectively.

Sex and Body Size

The results of the mixed model ANCOVA indicated a significant interaction effect of SVL*Sex (P=0.0357, DF=63, F=4.6056). Due to the significant interaction of SVL*Sex we separated male and female in all analyses thereafter. Using a mixed effect model with individual as a random factor, we found that body size (SVL) had a significant effect on LogMCP of males (P= 0.025, DF= 16) but not for females. Mixed model analyses of LogKDE failed to detect any significant effect of body size (SVL) at any level in either sex. In all Shapiro-Wilks analyses, SVL residuals met normality expectations.

Table 2 – Mixed model results of log transformed HR estimations and SVL separated by sex.

<u>SVL</u>	and a large		<u>StdDev</u> intercept	<u>StdDev</u> <u>Resid.</u>	<u>SE</u>	<u>t-value</u>	<u>p-value</u>	<u>EMM</u>	<u>df</u>
	Iviale		2 5 45 05	0.0000477	0.000464	2 474575	0.0240	2.04	40
		LOGIVICE	2.54E-05	0.6623477	0.009464	2.4/45/5	0.0249	3.01	10
		LogKDE 95%	7.66E-05	1.167635	0.016684	0.638394	0.5322	3.28	16
		LogKDE 90%	7.93E-05	1.179494	0.016854	0.602432	0.5553	3.04	16
		LogKDE 50%	7.64E-05	1.290133	0.018435	0.469614	0.645	1.75	16
	Female								
		LogMCP	0.5098357	0.6097318	0.01841	-0.9636	0.3402	1.91	47
		LogKDE 95%	0.6333774	0.8611593	0.024174	-1.80994	0.0767	2.01	47
		LogKDE 90%	0.6329975	0.8738886	0.024329	-1.8226	0.0747	1.76	47
		LogKDE 50%	0.6488621	0.959708	0.025763	-1.85432	0.07	0.433	47

Table 3 – Shapiro Wilks test of mixed model residuals of log transformed HR and SVL separated by sex.

SVL

Male		w	P-value
	LogMCP	0.97371	0.4364
	LogKDE 95%	0.95284	0.08169
	LogKDE 90%	0.95291	0.08251
	LogKDE 50%	0.95263	0.08026
Female			
	LogMCP	0.98261	0.3663

LogMCP	0.98261	0.3663
LogKDE 95%	0.98648	0.5828
LogKDE 90%	0.98637	0.5757
LogKDE 50%	0.98665	0.5935

A mixed model ANCOVA of BCI and Sex resulted in a significant interaction between BCI:Sex (P= 0.039, DF= 63, F= 4.449). Due to the BCI:Sex interaction we separated data by male and female for all analyses thereafter. Body condition index had significant effect on male log MCP HR size estimations using a mixed model analysis for LogMCP (P=0.0019, DF=16), SqrtKDE 95% (P=0.0564, DF=16), and SqrtKDE 90% (P=0.0582, DF=16). Our mixed model analyses failed to detect significant effects of body condition on female LogMCP or LogKDE (95%, 90%, and 50%). Among males, home range increased with improved body size. In all Shapiro-Wilk BCI analyses, residuals met normality expectations.

Table 4 – Mixed model results of log transformed and square root transformed HR estimations and BCI separated by sex.

<u>BCI</u>			<u>StdDev</u> intercept	<u>StdDev</u> <u>Resid.</u>	65	<u>t-value</u>	<u>p-value</u>	FNANA	<u>df</u>
			<u>(Rand.)</u>	<u>(Rand.)</u>	<u>5E</u>			EIVIIVI	
	Male								
		LogMCP	1.87E-05	0.6130828	1.25154	3.719404	0.0019	3.01	16
		SqrtKDE 95%	2.06E-04	3.039688	6.205183	2.056452	0.0564	5.32	16
		SqrtKDE 90%	1.93E-04	2.726955	5.566774	2.040143	0.0582	5.32	16
		LogKDE 50%	7.72E-05	1.241858	2.535114	1.846157	0.0835	1.75	16
	<u>Female</u>								
		LogMCP	0.5113251	0.6139191	2.137274	-0.12762	0.899	1.91	47
		LogKDE 95%	0.6680265	0.865878	2.95498	-0.93971	0.3522	2.02	47
		LogKDE 90%	0.6677329	0.8793367	2.988676	-0.92213	0.3612	1.77	47
		LogKDE 50%	0.684344	0.9677577	3.230188	-0.88796	0.3791	0.444	47

Table 5 – Shapiro Wilk test of mixed model residuals of log transformed and square root transformed HR and BCI separated by sex.

BCI			w	<u>P-value</u>
	Male			
		LogMCP	0.98193	0.7359
		SqrtKDE 95%	0.96862	0.2967
		SqrtKDE 90%	0.96884	0.3017
		LogKDE 50%	0.95235	0.07839
	<u>Female</u>			
		LogMCP	0.98642	0.5792
		LogKDE 95%	0.98439	0.4578
		LogKDE 90%	0.984	0.4366
		LogKDE 50%	0.98418	0.4465

Annual Variation

Effect of year on centroid was significant for all seven males and fourteen of the sixteen females. Using a Dunn-Sidak correction for n=23 (males=7; females=16) we applied an adjusted alpha level by of a'= 0.00214 (Wills and Beaupre 2000). Of the 23 individuals, all seven males and fourteen of sixteen females showed significant effects of year on home range centroid variation. The two females that were nonsignificant had centroids with an among year SD of centroid equal to 42.4m (ID 24) and 39.6m (ID 58). Comparatively, a female and male with three years of data and significant effects of year on centroid, had among year SD of centroid equal to 70.2m (ID 12) and 105.9m (ID 10), respectively. Additionally, ID 8 (P= 7.762e-14) had an among year SD of centroid of 143.1m.

ID	Sex	<u>Years</u>	<u>df</u>	<u>Pr (>F)</u>	Easting(SD)	<u>Northing(SD)</u>
5	f	5	4	3.14e-10 ***	84.78922	152.2456
8	f	5	4	7.762e-14 ***	183.2926	161.5384
11	f	3	2	6.124e-11 ***	136.6098	219.2296
12	f	3	2	6.21e-07 ***	70.23545	104.0421
14	f	7	6	6.339e-13 ***	126.3164	205.918
24	f	3	2	0.1247	77.99803	108.8823
31	f	3	2	5.66e-07 ***	173 5867	233 1548
33	f	5	4	2.2e-16 ***	119.0399	166.9463
37	f	3	2	7.562e-05	115 /068	113 0722
41	f	4	3	2.2e-16 ***	73 70094	133 9521
57	f	3	2	1.433e-06	122 0862	204 7607
58	f	3	2	0 4497	133.9802	158 0455
62	f	4	3	8.104e-09	120.5025	45 02102
63	f	Q	7	2 20 16 ***	120.3023	43.98102
65	1 f	8 7	6	2.2e-10 2.2e-16 ***	857 2778	1005 245
69	f	7	6	2.2e-16 2.2e-16 ***	157 0428	149 1265
2	m	6	5	2.2e-16 ***	225.3114	227.4274
3	m	3	2	5.125e-10	144 3574	1/3 7/71
Δ	m	3	2	0 004021 **	168 90/13	352 163
7	m	4	3	3.086e-05	200 2552	226 8250
9	m	6	5	5.154e-07 ***	200.3553	220.8259
10	m	3	2	2.349e-07 ***	107.0979	233,7775
45	m	3	2	4.875e-11 ***	167.7166	218.0522

Table 7 – MANOVA results of individual annual variation in HR.

Discussion

Our long-term study analyzed factors that influence the spatial ecology of the timber rattlesnake (annual variation, sex, SVL, and BCI). Our analyses showed inter-annual variability and suggested that snakes use portions of familiar habitat variably from year to year, (with appropriate temporal dispersion) n=25 is acceptable for calculating HR, and males have multiple factors that have a significant effect on HR size. Mixed model analyses on males using SVL as a covariate showed a significant increase in LogMCP HR estimates with increasing body size. Mixed model analyses of male BCI as a factor suggested a significant increase in LogMCP, SqrtKDE 95%, and SqrtKDE 90% as BCI improved.

Observation Requirements

Visual inspection of figure 2 shows, in general, an asymptote effect at *n*=25, when number of randomly sampled locations are plotted against MCP HR. A MCP area asymptote effect at approximately 25 observations determined our selection parameters to include only individuals with a minimum of 25 annual observations. However, we caution that location sampling densities must be spread evenly throughout the active season. It is well-known that habitat needs and usage of rattlesnakes varies seasonally (King & Duvall, 1990; Lind & Beaupre, 2015). Thus, as the active season progresses, it seems likely that home range may be affected until all basic seasonal functional needs of the snakes are met. For this reason, we caution that individual locations used to construct home ranges be distributed throughout the full active season, rather than constrained within narrow temporal windows. Our methods mirror those of Petersen (2019) in our selection of parameters individuals were required to meet for inclusion of this study. Peterson (2019) revealed an asymptote effect at 60 locations points whereas our asymptote selections. We explain our

21

difference to Peterson by the contrast in tracking efforts (Petersen 5-7 days/week; this study 1-2 days/week). In our view, the unifying concept underlying best sampling practice is that regardless of sampling interval, samples distributed across the full active season are required to estimate home range.

Sex

The result of our linear mixed effect model showed a significant interaction between SVL and Sex. A significant interaction of SVL:sex violates the assumption of slope homogeneity which can be attributed to sexual dimorphic behavior seen in *C.horridus* as males increase in body size, they engage in mate searching, typically resulting in larger HR. Female reproductive strategy however, conserves energy by forcing males to seek them out (Duvall et al., 1992b). Petersen (2019) specifically reported male TR increased their late summer distances moved in alignment with male participation in mate-searching behavior; while others identified male snakes as having larger home range estimates compared to females (Adams, 2005; Durbian et al., 2008; Hyslop et al., 2014). Petersen used body size as factor while others separated based on sex. In contrast to this study, none of the studies mentioned prior justified separation of sex by using a slope homogeneity test of SVL:sex.

Body Size

In males, our mixed model analysis showed that SVL has a significant effect on the MCP HR but no effects on KDE (95%, 95% and 50%). The MCP method detected this effect because it includes 100% of data points, suggesting that Kernel estimates may be too conservative by

22

eliminating 5% of the most extreme locations. Mate searching in our population can consist of both long and short movements generally over 2-3 weeks in mid to late summer before returning to more commonly used areas often nearer to overwintering hibernacula. Mid to late summer movements are associated with reproductive males in positive body condition who actively search for receptive females (Lind & Beaupre, 2015). Location data collected during mate searching movements are potentially eliminated in the KDE estimation because some may fall outside of the 95%, 90% and 50% isopleths. By excluding exterior points from HR estimations, KDE methods potentially fail to incorporate highly relevant patches of habitat that snakes may use predominantly for the functionally-dedicated activity of mate search (King & Duvall, 1990). We agree with Row and Blouin-Demers (2006b) that kernel estimates are poor tools to use in examining home range size and are likely better applied to the analysis of activity within a home range.

Body Condition

Body condition index is used to assess recent environmental resource quality with the assumption that resources acquired by individuals predict engagement in activities such as reproduction. Similar to side-blotched lizards (Scoular et al., 2011) and Massasauga Rattlesnakes (Wastell & Mackessy, 2011), our findings suggest that improved BCI as a result of ecosystem productivity is an important factor influencing annual HR size of male Timber Rattlesnakes. Our analysis suggests that a rise in BCI or mass-energy status of individual male snakes significantly increases LogMCP and SqrtKDE (95%, 90%) HR. Our result can be explained by participation in mate searching behavior seen in males and the potential need to increase foraging effort to meet the energy requirements associated with a larger body size

(Petersen et al., 2019; Lind & Beaupre, 2015; McNab, 1963). Foraging success and efficient use of prey items within an individual's HR to meet energetic requirements are necessary along with the expansion of HR size to maintain a sufficient prey population (assuming that prey is not abundant; McNab, 1963). As males grow, their ability to feed on larger prey items becomes more diverse. For example, a snake that is 90 cm (Clark, 2002) has the potential to feed on prey items such as grey squirrels. Because not all snakes (male or female) are large enough to ingest a squirrel, larger snakes are able to incorporate a new prey population into their diet with limited intraspecific competition. By increasing their potential prey population individuals may then benefit by relying on smaller foraging area as a result. Though a smaller foraging area in larger males as a result of increased prey population does not explain the larger MCP HR, it may explain the size of core use areas identified by the 50% KDE isopleth. Males with improved body condition that have met their energetic requirements for growth, maintenance, and storage will allocate excess energy towards reproductive efforts such as sperm production, mate searching, male-to-male combat and mate guarding/defense (Beaupre & Douglas, 2009). In our study system, as reported in Lind and Beaupre (2015), male C. horridus with improved body condition had higher circulating testosterone concentrations, higher participation in mate-search behavior, and allocated less time toward energy acquisition. With 100% MCP generated strictly from breeding season locations as a mate search variable, Lind and Beaupre (2015) showed decline in late summer MCP during a year with significantly lower testosterone concentrations compared to other years. Additionally, males appear to participate in mate search at different effort levels according to what energetic capital is available to them from high to low amounts rather than an all or nothing response (Lind & Beaupre, 2015).

24

Annual Variation

Annual variation of home range in this study is consistent with the findings of Sonoran Desert tortoises (Sullivan et al., 2016), side-blotched lizards (Scoular et al., 2011), loggerhead turtles (Hawkes et al., 2011), and box turtles (Roe et al., 2020) in that Timber Rattlesnakes show repeated HR fidelity and often have overlapping potions from year to year. However, our results show that year had a significant effect in 21 of 23 individuals, suggesting that a single year of HR range analysis or a short-term study may not be sufficient to estimate an individual's HR with accuracy. It is important to note that the Dunn-Sidak correction for experimentwise error is conservative if differences are indeed demonstrated, suggesting that we have high confidence that HR centroid location varies significantly from year to year in *C. horridus*. The annual variability in location of an individual's HR center can be explained by factors such as habitat disturbances, reproductive condition and resource abundance, such as, reproductive females, prey abundance, and available thermoregulatory habitat (Waldron et al., 2006).

Body condition of males as well as the density or proximity of receptive females is likely to have a strong effect on the annual shifts in home range centroid (Lind and Beaupre, 2015). Following a resource limited year, it is possible that there are fewer receptive females that also occur in lower densities, spread across the study site (Beaupre, 2008). Under such circumstances reproductive males might potentially travel further distances in search of females who are receptive, or conversely may not search at all. However, if a male is in poorer body condition, participation in reproductive activity such as mate search is likely to decrease rather than experience an all or nothing response (Lind & Beaupre, 2015). Annual variation of home range centroid may also be caused by fluctuations in prey abundance from one area of the study site to the next. Prey densities also vary annually based upon natural and anthropogenic disturbances such as fire, both wild and controlled (Beaupre & Douglas, 2009, 2012), logging or clear cutting, severe winds, and winter ice storms. Annual variation in prey abundance is directly tied to the fluctuations in small-mammal populations dependent on acorn mast produced by oak trees (Beaupre & Douglas, 2009; Wolff, 1996). Disturbances can also affect habitat thermodynamics. Fire, severe wind, winter storms, and logging methods are capable of thinning or removing completely the forest canopy and causing an alteration in the available thermal habitat. In addition, the lack of disturbances such as fire, that serve as a key mechanism of forest ecology, can allow cedar trees to encroach on rocky outcroppings, glades, and bluffs, casting shade and altering the thermal conditions over longer time spans.

Overall, our findings mirror similar Timber Rattlesnake home range studies in that males exhibit larger HR sizes compared to non-gravid females (Reinert and Zappalorti, 1988; Rudolph and Burgdorf, 1997; Brown, 1993; Sealy, 2002; Adams 2005, MacGowan and Walker, 2013, Waldron et al, 2006). Mean MCP HR results from our study (males 25.77 ha., non-gravid females 9.41 ha., SE 3.70 and 1.60 respectively) favorably compare to North Carolina (males 40.15 ha.,non-gravid females 14.1 ha., SE 24.65 and 3.10 respectively; Sealy 2002), and Wisconsin (Males 21.1 ha., non-gravid females 13.3 ha., SE 9.29 and 5.40 respectively; Hamilton 2009) but were much smaller than studies in Indiana (males 65.7 ha., non-gravid females 20.6, SE 9.8 and 5.9 respectively; MacGowan and Walker 2013), West Virginia (males 94.3 ha. and non-gravid females 31.2 ha., SE 23.0 and 5.54 respectively; Adams' 2005) and Missouri (males 96.3 ha., nongravid females 17.6 ha, SE 30.17 and 12.9 respectively; Wittenberg 1999). Varying results among studies may be explained by factors such as age, body size, BCI, regionally specific duration of active season, fluctuations in resource densities, habitat patchiness, and habitat quality (Gregory et al, 1987;. Harestad and Bunnell, 1979; McNab, 1963). The temporal spread of location data points collected through monitoring effort can influence HR and animal movement studies as reported and discussed here. Our findings are in line with those of Hawkes (2011) in that animals create common patterns of temporal movements that are dependent on season and posits the idea that location data must be distributed evenly across the active season in order to fully capture the relevant biological activity. Because critical functionally-dedicated episodic activities and their associated movements occur throughout their active season, Timber Rattlesnakes exemplify this need. Failure to include an activity season in its entirety likely underestimates HR (Maag, 2017). Petersen (2019) required a minimum number of 60 locations to capture HR variability across an active season; whereas our study determined a sampling regime of only 25 minimum locations necessary to capture seasonal HR variability. The contrast in minimum sampling requirements between this study and Petersen (2019) is explained by the frequency of sampling over the duration of a full active season. Petersen (2019) sampling effort collected 5-7 individual locations per week with an average of 194.7 locations collected per year; whereas our study collected individual's locations 2-3 times per week with an average of 30.6 locations collected per year. Home range varies among individuals and from year-to-year, and as a result, it requires several years of monitoring effort to fully capture habitat use patterns of a population. Studies of limited sample size or short duration (1-2 years, typical of most telemetry studies) are likely to underestimate the lifetime HR area used by a Timber Rattlesnake. Sampling methods that lack relevant temporal dispersion or adequate sample size increase the risk of failing to identify habitat features that may be critically important for local management conservation efforts.

Furthermore, long term data sets illuminate the inter-annual flexibility of long-lived vertebrates as they interact with dynamic local environments.

Our findings suggest that improved BCI as a result of ecosystem productivity is an important factor influencing annual HR size of male TRs. Adequate temporal sampling over the duration of many years and from a large sample size is necessary to estimate HR size in a way that is useful to conservation efforts. We define adequate temporal sampling as evenly dispersed collection of location data across active seasons. Additionally, we echo the findings of Row and Blouin-Demers in that MCP estimates of HR size are preferred over kernel density estimates; as KDEs have the potential to eliminate functionally-relevant locations.

References

- Adams, J.P.(2005).Home range and behavior of the timber rattlesnake (Crotalus horridus) [M.S., Marshall University].In *ProQuest Dissertations and Theses* (305356625).ProQuest Dissertations & Theses Global.https://www.proquest.com/dissertations-theses/homerange-behavior-timber-rattlesnake-i-crotalus/docview/305356625/se-2?accountid=8361
- Agugliaro, J.(2011). *Ecophysiology of hibernation in timber rattlesnakes (crotalus horridus)*. University of Arkansas, Fayetteville.
- Barbour, M.G., & Billings, W.D.(2000). North American terrestrial vegetation. Cambridge University Press.
- Beaupre, S.(2008). Annual variation in time-energy allocation by timber rattlesnakes (Crotalus horridus) in relation to food acquisition. *The Biology of Rattlesnakes*, 111–122.
- Beaupre, S.(2016).Novel tracking and remote monitoring technologies: Applications to studying wild rattlesnakes.*Rattlesnakes of Arizona*, 2, 345–363.
- Beaupre, S., & Douglas, L.E.(2009).9.Snakes as Indicators and Monitors of Ecosystem Properties (S.J.Mullin & R.A.Seigel, Eds.; pp.244–261).Cornell University Press.https://doi.org/10.7591/9780801459092-013
- Beaupre, S., & Douglas, L.E.(2012). *Responses of timber rattlesnakes to fire: Lessons from two prescribed burns*. 192–204.
- Beaupre, S., & Duvall, D.J.(1998).Integrative biology of rattlesnakes.*Bioscience*, 48(7), 531–538.
- Beaupre, S.(2008). Annual variation in time-energy allocation by timber rattlesnakes (Crotalus horridus) in relation to food acquisition. *The Biology of Rattlesnakes*, 111–122.
- Beck, D.D.(1995).Ecology and Energetics of Three Sympatric Rattlesnake Species in the Sonoran Desert.*Journal of Herpetology*, 29(2), 211– 223.JSTOR.https://doi.org/10.2307/1564558
- Blair, W.F.(1940).Home Ranges and Populations of the Meadow Vole in Southern Michigan.*The Journal of Wildlife Management*, 4(2), 149–161.JSTOR.https://doi.org/10.2307/3795652

- Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., & Robinson, W.D.(2011).Technology on the move: Recent and forthcoming innovations for tracking migratory birds.*BioScience*, 61(9), 689–698.
- Brito, J.C.(2003).Seasonal variation in movements, home range, and habitat use by male Vipera latastei in northern Portugal.*Journal of Herpetology*, *37*(1), 155–160.
- Brown, G.P., & Weatherhead, P.J.(1999).Female distribution affects mate searching and sexual selection in male northern water snakes (Nerodia sipedon).*Behavioral Ecology and Sociobiology*, 47(1), 9–16.
- Brown, W.S., Pyle, D.W., Greene, K.R., & Friedlaender, J.B.(1982).Movements and Temperature Relationships of Timber Rattlesnakes (Crotalus horridus) in Northeastern New York.*Journal of Herpetology*, 16(2), 151– 161.JSTOR.https://doi.org/10.2307/1563808
- Browning, D.M., Beaupre, S.J., & Duncan, L.(2005).Using partitioned Mahalanobis D2 (k) to formulate a GIS-based model of timber rattlesnake hibernacula.*The Journal of Wildlife Management*, 69(1), 33–44.
- Burt, W.H.(1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24(3), 346–352.
- Cagle, F.R.(1944). Home range, homing behavior, and migration in turtles.
- Carfagno, G.L., & Weatherhead, P.J.(2008). Energetics and space use: Intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes. *Journal of Animal Ecology*, 416–424.
- Clark, R.W.(2002).Diet of the timber rattlesnake, Crotalus horridus.*Journal of Herpetology*, *36*(3), 494–499.
- Clark, R.W., Schuett, G.W., Repp, R.A., Amarello, M., Smith, C.F., & Herrmann, H.-W.(2014).Mating systems, reproductive success, and sexual selection in secretive species: A case study of the western diamond-backed rattlesnake, Crotalus atrox.*PLoS One*, 9(3), e90616.
- Cochran, W.W., & Lord, R.D.(1963). A Radio-Tracking System for Wild Animals. *The Journal of Wildlife Management*, 27(1), 9–24. JSTOR. https://doi.org/10.2307/3797775

- Danna L.Baxley & Carl P.Qualls.(2009).Black Pine Snake (Pituophis melanoleucus lodingi): Spatial Ecology and Associations between Habitat Use and Prey Dynamics.*Journal of Herpetology*, 43(2), 284–293.https://doi.org/10.1670/08-074R1.1
- Durant, S.M.(2000a).Living with the enemy: Avoidance of hyenas and lions by cheetahs in the Serengeti.*Behavioral Ecology*, *11*(6), 624–632.
- Durant, S.M.(2000b).Predator avoidance, breeding experience and reproductive success in endangered cheetahs, Acinonyx jubatus.*Animal Behaviour*, 60(1), 121–130.
- Durbian, F.E., King, R.S., Crabill, T., LAMBERT-DOHERTY, H., & Seigel, R.A.(2008).Massasauga home range patterns in the Midwest.*The Journal of Wildlife Management*, 72(3), 754–759.
- Duvall, D., Arnold, S.J., & Schuett, G.W.(1992a). Pitviper mating systems: Ecological potential, sexual selection, and microevolution. *Biology of the Pitvipers*, 321–336.
- Duvall, D., Arnold, S., & Schuett, G.W.(1992b).Pitviper mating systems: Ecological potential, sexual selection, and microevolution.*Biology of the Pitvipers*, 321–336.
- Dyer, J.M.(2006).Revisiting the Deciduous Forests of Eastern North America.*BioScience*, 56(4), 341–352.https://doi.org/10.1641/0006-3568(2006)56[341:RTDFOE]2.0.CO;2
- Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., & Calabrese, J.M.(2015).Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator.*Ecology*, 96(5), 1182–1188.https://doi.org/10.1890/14-2010.1
- Forman, R.T.T., & Godron, M.(1981).Patches and Structural Components for A Landscape Ecology.*BioScience*, *31*(10), 733–740.https://doi.org/10.2307/1308780
- Gardiner, L.E., Somers, C.M., Martino, J.A., Parker, D.L., & Poulin, R.G.(2013).Balancing the dumbbell: Summer habitats need protection in addition to winter dens for northern snake communities.*The Journal of Wildlife Management*, 77(5), 975– 982.https://doi.org/10.1002/jwmg.555
- Gardner-Santana, L.C., & Beaupre, S.J.(2009). Timber rattlesnakes (Crotalus horridus) exhibit elevated and less variable body temperatures during pregnancy. *Copeia*, 2009(2), 363–368.
- Graves, B.M., & Duvall, D.(1993).Reproduction, rookery use, and thermoregulation in freeranging, pregnant Crotalus v.Viridis.*Journal of Herpetology*, 33–41.
- Greene, H.W., May, P.G., Hardy Sr, D.L., Sciturro, J.M., & Farrell, T.M.(2002).Parental behavior by vipers.*Biology of the Vipers*, 179–205.
- Hansteen, T.L., Andreassen, H.P., & Ims, R.A.(1997).Effects of Spatiotemporal Scale on Autocorrelation and Home Range Estimators.*The Journal of Wildlife Management*, 61(2), 280–290.JSTOR.https://doi.org/10.2307/3802583
- Hardy Sr, D., & Greene, H.(1999).Surgery on rattlesnakes in the field for implantation of transmitters.*Sonoran Herpetologist*, *12*(3), 25–27.
- Hawkes, L.A., Witt, M.J., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M., Frick, M.G., Godfrey, M.H., Griffin, D.B., & Murphy, S.R.(2011). Home on the range: Spatial ecology of loggerhead turtles in Atlantic waters of the USA. *Diversity and Distributions*, 17(4), 624–640.
- Hayne, D.W.(1949).Calculation of Size of Home Range.*Journal of Mammalogy*, 30(1), 1–18.JSTOR.https://doi.org/10.2307/1375189
- Horner, M.A., & Powell, R.A.(1990).Internal Structure of Home Ranges of Black Bears and Analyses of Home-Range Overlap.*Journal of Mammalogy*, 71(3), 402– 410.https://doi.org/10.2307/1381953

Hoss, S.K., Guyer, C., Smith, L.L., & Schuett, G.W.(2010).Multiscale Influences of Landscape Composition and Configuration on the Spatial Ecology of Eastern Diamond-backed Rattlesnakes (Crotalus adamanteus).*Journal of Herpetology*, 44(1), 110–123.JSTOR.
Huey, R.B.(1982).*Temperature, physiology, and the ecology of reptiles*.Biology of the Reptilia.

Hundertmark, K.J.(1998). Home range, dispersal and migration. *Ecology and Management of the* North American Moose. Smithsonian Institution Press, Washington, DC, USA, 303–335.

Hyslop, N.L., Meyers, J.M., Cooper, R.J., & Stevenson, D.J.(2014).Effects of body size and sex of Drymarchon couperi (eastern indigo snake) on habitat use, movements, and home range size in Georgia.*The Journal of Wildlife Management*, 78(1), 101–111.https://doi.org/10.1002/jwmg.645

- Kaczensky, P., Ito, T.Y., & Walzer, C.(2010).Satellite Telemetry of Large Mammals in Mongolia: What Expectations Should We Have for Collar Function? *Wildlife Biology in Practice (Online)*, 6(2), 108–126.PubMed.https://doi.org/10.2461/wbp.2010.6.9
- Kapfer, J.M., Pekar, C.W., Reineke, D.M., Coggins, J.R., & Hay, R.(2010).Modeling the relationship between habitat preferences and home-range size: A case study on a large mobile colubrid snake from North America.*Journal of Zoology*, 282(1), 13– 20.https://doi.org/10.1111/j.1469-7998.2010.00706.x
- Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J.-M., & Moorcroft, P.R.(2010). The home-range concept: Are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2221– 2231.https://doi.org/10.1098/rstb.2010.0093
- King, M.B., & Duvall, D.(1990).Prairie rattlesnake seasonal migrations: Episodes of movement, vernal foraging and sex differences.*Animal Behaviour*, 39(5), 924– 935.https://doi.org/10.1016/S0003-3472(05)80957-1
- Lind, C.M., & Beaupre, S.J.(2015).Male Snakes Allocate Time and Energy according to Individual Energetic Status: Body Condition, Steroid Hormones, and Reproductive Behavior in Timber Rattlesnakes, Crotalus horridus.*Physiological and Biochemical Zoology*, 88(6), 624–633.https://doi.org/10.1086/683058
- Loehle, C., & Li, B.-L.(1996).Habitat Destruction and the Extinction Debt Revisited.*Ecological Applications*, 6(3), 784–789.JSTOR.https://doi.org/10.2307/2269483
- Maag, D.W.(2017). The spatial ecology and microhabitat selection of the Pygmy Rattlesnake (Sistrurus miliarius) in Southwestern Missouri.
- MacArthur, R.H., & Pianka, E.R.(1966).On optimal use of a patchy environment.*The American Naturalist*, *100*(916), 603–609.
- MacGowan, B.J., & Walker, Z.J.(2013).Spatial ecology of timber rattlesnakes on the Hardwood Ecosystem Experiment: Pre-treatment results.*In: Swihart, Robert K.; Saunders, Michael R.; Kalb, Rebecca A.; Haulton, G.Scott; Michler, Charles H., Eds.2013.The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management.Gen.Tech.Rep.NRS-P-108.Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station: 86-94., 86–94.*

- McNab, B.K.(1963).Bioenergetics and the determination of home range size.*The American Naturalist*, 97(894), 133–140.
- Miller, G.J., Smith, L.L., Johnson, S.A., & Franz, R.(2012).Home Range Size and Habitat Selection in the Florida Pine Snake (Pituophis melanoleucus mugitus).*Copeia*, 2012(4), 706–713.https://doi.org/10.1643/CE-12-054
- Moore, J.A., & Gillingham, J.C.(2006).Spatial Ecology and Multi-scale Habitat Selection by a Threatened Rattlesnake: The Eastern Massasauga (Sistrurus Catenatus Catenatus).*Copeia*, 2006(4), 742–751.https://doi.org/10.1643/0045-8511(2006)6[742:SEAMHS]2.0.CO;2
- Odum, E.P., & Kuenzler, E.J.(1955). Measurement of Territory and Home Range Size in Birds. *The Auk*, 72(2), 128–137. JSTOR. https://doi.org/10.2307/4081419
- Petersen C., Scott M.Goetz, Michael J.Dreslik, John D.Kleopfer, & Alan H.Savitzky.(2019).Sex, Mass, and Monitoring Effort: Keys to Understanding Spatial Ecology of Timber Rattlesnakes (Crotalus horridus).*Herpetologica*, 75(2), 162– 174.https://doi.org/10.1655/D-18-00035
- Powell, R.A.(2000). Animal home ranges and territories and home range estimators. *Research Techniques in Animal Ecology: Controversies and Consequences*, 442, 65–110.
- Quinn, H., & Jones, J.(1974). Squeeze box technique for measuring snakes. *Herpetological Review*, 5(2), 35.
- Reed, R.N., & Douglas, M.E.(2002). Ecology of the grand canyon rattlesnake (Crotalus viridis abyssus) in the Little Colorado River Canyon, Arizona. *The Southwestern Naturalist*, 30– 39.
- Reinert, H.K., & Cundall, D.(1982). An Improved Surgical Implantation Method for Radio-Tracking Snakes. *Copeia*, 1982(3), 702–705. JSTOR. https://doi.org/10.2307/1444674
- Rodgers, A.R.(2001).Tracking animals with GPS: the first 10 years.*Tracking Animals with GPS*, *1*.
- Roe, J., Kish, A., & Nacy, J.(2020). Variation and repeatability of home range in a forestdwelling terrestrial turtle: Implications for prescribed fire in forest management. *Journal* of Zoology, 310(1), 71–82.

- Row, J.R., & Blouin-Demers, G.(2006).Kernels Are Not Accurate Estimators of Home-range Size for Herpetofauna.*Copeia*, 2006(4), 797–802.https://doi.org/10.1643/0045-8511(2006)6[797:KANAEO]2.0.CO;2
- Samuel, M.D., Pierce, D.J., & Garton, E.O.(1985).Identifying Areas of Concentrated Use within the Home Range.*Journal of Animal Ecology*, *54*(3), 711–719.JSTOR.https://doi.org/10.2307/4373
- Schofield, G., Hobson, V.J., Lilley, M.K.S., Katselidis, K.A., Bishop, C.M., Brown, P., & Hays, G.C.(2010).Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management.*Biological Conservation*, 143(3), 722– 730.https://doi.org/10.1016/j.biocon.2009.12.011
- Scoular, K.M., Caffry, W.C., Tillman, J.L., Finan, E.S., Schwartz, S.K., Sinervo, B., & Zani, P.A.(2011).Multiyear home-range ecology of common side-blotched lizards in eastern Oregon with additional analysis of geographic variation in home-range size.*Herpetological Monographs*, 25(1), 52–75.
- Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., & Gitzen, R.A.(1999).Effects of Sample Size on Kernel Home Range Estimates.*The Journal of Wildlife Management*, 63(2), 739–747.JSTOR.https://doi.org/10.2307/3802664
- Seaman, D.E., & Powell, R.A.(1996). An Evaluation of the Accuracy of Kernel Density Estimators for Home Range Analysis. *Ecology*, 77(7), 2075– 2085.https://doi.org/10.2307/2265701

Silverman, B.W.(2003). Density estimation for statistics and data analysis. Routledge.

Sokal, R., & Rohlf, F.(1981). Biometry Second Edition WH Freeman and Company. New York.

- Stevens, M.A., & Barry, R.E.(2002). Selection, size, and use of home range of the Appalachian cottontail, Sylvilagus obscurus. *Canadian Field-Naturalist*, 116(4), 529–535.
- Sullivan, B.K., Owens, A.K., Sullivan, K.O., & Sullivan, E.A. (2016). Spatial ecology of Sonoran desert tortoises (Gopherus morafkai): I.Fidelity in home range, refuge use and foraging behavior. *Journal of Herpetology*, 50(4), 509–519.
- Swihart, R.K., & Slade, N.A.(1985a).Influence of Sampling Interval on Estimates of Home-Range Size.*The Journal of Wildlife Management*, 49(4), 1019– 1025.JSTOR.https://doi.org/10.2307/3801388

- Tilman, D., May, R.M., Lehman, C.L., & Nowak, M.A.(1994). Habitat destruction and the extinction debt. *Nature*, *371*(6492), 65–66. https://doi.org/10.1038/371065a0
- Waldron, J.L., Lanham, J.D., & Bennett, S.H.(2006).USING BEHAVIORALLY-BASED SEASONS TO INVESTIGATE CANEBRAKE RATTLESNAKE (CROTALUS HORRIDUS) MOVEMENT PATTERNS AND HABITAT SELECTION.*Herpetologica*, 62(4), 389–398.https://doi.org/10.1655/0018-0831(2006)62[389:UBSTIC]2.0.CO;2
- Wastell, A.R., & Mackessy, S.P.(2011).Spatial Ecology and Factors Influencing Movement Patterns of Desert Massasauga Rattlesnakes (Sistrurus catenatus edwardsii) in Southeastern Colorado.*Copeia*, 2011(1), 29–37.https://doi.org/10.1643/CE-09-122
- Webb, J.K., & Shine, R.(1997). A field study of spatial ecology and movements of a threatened snake species, Hoplocephalus bungaroides. *Biological Conservation*, 82(2), 203–217.https://doi.org/10.1016/S0006-3207(97)00032-3
- Wills, C.A., & Beaupre, S.J.(2000). An Application of Randomization for Detecting Evidence of Thermoregulation in Timber Rattlesnakes (Crotalus horridus) from Northwest Arkansas. *Physiological and Biochemical Zoology*, 73(3), 325– 334.https://doi.org/10.1086/316750
- Wolff, J.O.(1996).Population Fluctuations of Mast-Eating Rodents Are Correlated with Production of Acorns.*Journal of Mammalogy*, 77(3), 850– 856.https://doi.org/10.2307/1382690
- Worton, B.J.(1989).Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies.*Ecology*, 70(1), 164–168.https://doi.org/10.2307/1938423



Figure 2 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 2 in year 2002, 2006, 2007, 2008, and 2009.



Figure 3 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 3 in year 2009 and 2010.



Figure 4 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 4 in year 2008 and 2009.



Figure 5 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 5 in year 2001, 2002, and 2003.



Figure 6 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 8 in year 2007, 2008, 2009, and 2010.



Figure 7 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 9 in year 2006, 2007, 2008, and 2009.



Figure 8 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 10 in year 2000, 2001, and 2002.



Figure 9 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 11 in year 2001.



Figure 10 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 12 in year 2000, 2001, and 2002.



Figure 11 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 13 in year 2006 and 2007.



Figure 12 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 14 in year 2001, 2002, 2003, 2004, 2005, 2006, and 2007.



Figure 13 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 15 in year 2000.



Figure 14 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 16 in year 2000.



Figure 15 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 24 in year 2008 and 2009.



Figure 16 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 25 in year 2008 and 2009.



Figure 17 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 26 in year 2009 and 2010.



Figure 18 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 27 in year 2009.



Figure 19 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 28 in year 2008.



Figure 20 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 29 in year 2006.



Figure 21 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 30 in year 2010.



Figure 22 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 31 in year 2008 and 2009.



Figure 23 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 33 in year 2003, 2004, and 2005.



Figure 24 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 34 in year 2003.



Figure 25 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 35 in year 2003 and 2004.



Figure 26 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 36 in year 2003 and 2004.



Figure 27 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 37 in year 2006 and 2008.



Figure 28 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 38 in year 2008.



Figure 29 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 39 in year 2009.



Figure 30 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 40 in year 2001.



Figure 31 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 41 in year 2001, 2003, and 2004.



Figure 32 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 42 in year 2003.


Figure 33 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 43 in year 2003 and 2004.



Figure 34 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 44 in year 2001.



Figure 35 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 45 in year 2008 and 2009.



Figure 36 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 47 in year 2006 and 2007.



Figure 37 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 51 in year 2006.



Figure 38 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 52 in year 2001, 2002, and 2004.



Figure 39 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 53 in year 2001, 2002, and 2004.



Figure 40 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 54 in year 2000.



Figure 41 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 55 in year 2005.



Figure 42 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 57 in year 2000 and 2002.



Figure 43 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 58 in year 2000, 2001, and 2002.



Figure 44 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 59 in year 2001.



Figure 45 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 60 in year 2001, 2002, and 2003.



Figure 46 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 61 in year 2005.



Figure 47 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 62 in year 2000, 2001, 2003, and 2004.



Figure 48 – *Minimum convex polygon estimation and den location for Timber Rattlesnake ID* 63 *in year 2000, 2001, 2002, 2004, 2005, 2006, 2007, and 2008.*



Figure 49 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 64 in year 2000.



Figure 50 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 65 in year 2005, 2006, 2007, 2009, and 2010



Figure 51 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 66 in year 2002 and 2003.



Figure 52 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 67 in year 2001.



Figure 53 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 68 in year 2000, 2001, and 2002.



Figure 54 – *Minimum convex polygon estimation and den location for Timber Rattlesnake ID* 69 *in year 2002, 2003, 2004, 2005, 2006, 2007, and 2009.*



Figure 55 – Minimum convex polygon estimation and den location for Timber Rattlesnake ID 70 in year 2000.

Table 8 – Appendix data

ID	PIT	Sex	Year	Mass (g)	SVL (cm)	MCP (ha.)	KDE95 (ha.)	KDE90 (ha.)	KDE50 (ha.)
2	035-865-037	m	2002	486.25	80.4	15.1953	21.89847	18.21084	5.438994
2	035-865-037	m	2006	557.22	87.4	43.97525	40.4557	31.13016	6.869868
2	035-865-037	m	2007	571.87	85.8	27.52155	84.25302	67.81448	21.26418
2	035-865-037	m	2008	452.95	89.7	11.07785	10.08574	7.871451	1.825439
2	035-865-037	m	2009	439.29	89.1	20.2427	9.453458	7.083617	1.299712
3	051-381-824	m	2009	475.55	86.9	15.9247	48.09715	35.96262	10.59042
3	051-381-824	m	2010	433.07	89.2	8.64755	5.184391	3.989573	0.975348
4	035-872-614	m	2008	1678.3	108.1	22.4065	4.962604	3.760413	0.818008
4	035-872-614	m	2009	1227.18	108.4	74.0194	82.11174	63.93114	20.43313
5	035-854-525	f	2001	253.65	68.7	7.30685	22.62072	17.8901	5.534704
5	035-854-525	f	2002	332.09	70.9	5.0222	7.321926	5.968912	1.720589
5	035-854-525	f	2003	391.7	73.9	4.27815	5.321279	4.143647	1.108332
8	065-825-888	f	2007	442.4	80.3	17.50255	16.09422	12.77582	3.594941
8	065-825-888	f	2008	454.37	81.5	17.07915	29.9523	23.91657	7.25281
8	065-825-888	f	2009	459.21	81.5	27.20175	61.65259	48.42081	14.93224
8	065-825-888	f	2010	471.87	84.1	16.80635	7.438785	5.611991	1.172082
9	065-844-623	m	2006	529.02	88.3	5.2747	7.743344	6.066364	1.483736
9	065-844-623	m	2007	518.01	88.8	18.6674	34.66835	28.21241	9.451612
9	065-844-623	m	2008	797.08	92	32.3981	77.56367	61.66178	16.71466
9	065-844-623	m	2009	969.45	92.9	61.68645	50.59068	39.4803	9.338225
10	027-057-600	m	2000	395	78.1	14.86765	61.77623	49.68272	17.40462
10	027-057-600	m	2001	366.9	78.2	14.73555	61.93128	49.75915	17.41518
10	027-057-600	m	2002	567.15	81	25.153	39.74558	32.32675	10.43423
11	027-051-350	f	2001	341.8	78.2	3.01565	10.1289	8.178044	2.481971
12	027-077-513	f	2000	363	74.9	6.7111	8.796947	7.238172	2.244742
12	027-077-513	f	2001	363.5	76	2.2982	2.199563	1.729238	0.516703
12	027-077-513	f	2002	436.82	77.2	0.66885	1.035121	0.795515	0.164083
13	035-857-097	f	2006	379.67	81.8	4.6364	6.893389	5.483812	1.352835

13	035-857-097	f	2007	377.33	82.6	6.40745	9.326376	7.397119	2.264167
14	036-040-030	f	2001	324.3	73	6.43485	16.57773	13.50517	4.413797
14	036-040-030	f	2002	362.14	75.7	17.95675	3.234018	2.469493	0.58608
14	036-040-030	f	2003	281.2	76	13.9039	5.186072	4.121908	1.11218
14	036-040-030	f	2004	294.39	75.7	16.2049	43.27287	34.67173	10.9576
14	036-040-030	f	2005	396	77.4	16.43025	28.85495	23.36458	7.158246
14	036-040-030	f	2006	343.75	77.6	14.59395	10.53386	8.273132	2.120105
14	036-040-030	f	2007	317.4	78.2	12.2257	4.136719	3.228657	0.854607
15	027-086-300	f	2000	468	78.7	12.054	21.45607	16.51818	2.912165
16	027-095-368	f	2000	333.14	81.3	6.8516	8.60924	6.709054	1.309154
24	096-799-612	f	2008	448.44	74.5	3.17595	7.217293	5.803325	1.846837
24	096-799-612	f	2009	364.0233	75	11.78605	20.88793	17.07079	4.786829
25	096-636-125	m	2009	715.18	97.9	22.9272	25.50761	20.56444	5.945345
26	096-616-605	m	2009	637.33	84.1	35.36705	91.80885	74.74755	25.02177
26	096-616-605	m	2010	566	83.8	24.7499	72.13432	57.66274	17.59792
27	096-611-093	f	2009	383.95	79.1	7.8853	9.324067	7.21272	1.852084
28	096-595-609	m	2008	1098.5	105.3	9.94435	19.73478	16.28821	4.844
29	096-595-364	m	2006	233.89	74.1	3.6101	5.039652	4.05718	1.278929
30	096-600-838	m	2010	697.83	90.7	10.74625	21.18606	17.13817	5.001216
31	065-844-623	f	2008	333.14	80.2	23.3981	77.56367	61.66178	16.71466
31	065-844-623	f	2009	468	80.1	61.68645	50.59068	39.4803	9.338225
33	051-267-860	f	2003	514.79	97	4.39435	1.844592	1.422077	0.327758
33	051-267-860	f	2004	786.005	95.2	7.72835	13.45829	10.80592	2.787915
33	051-267-860	f	2005	893.11	97.5	15.06185	1.173775	0.877873	0.130452
34	051-126-550	f	2003	391.16	78.2	3.6721	0.496299	0.392679	0.099407
35	051-086-267	f	2003	349.6	75.4	6.9916	6.511882	4.934354	1.069923
35	051-086-267	f	2004	296.6433	76.9	1.11005	1.154611	0.914906	0.280878
36	051-065-004	f	2003	297.14	73.2	15.64885	9.465121	7.46563	1.905169
36	051-065-004	f	2004	239.26	74.2	9.121	17.94645	13.62472	3.260282
37	036-259-363	f	2006	374.82	90.5	5.2722	2.962647	2.280767	0.547508
37	036-259-363	f	2008	327.36	90.7	3.21245	1.730262	1.3664	0.39499

38	051-076-874	m	2008	403.835	81.9	20.84515	2.810803	2.158953	0.444287
39	036-111-850	m	2009	1133.863	108.8	13.8863	19.11621	14.75315	4.088321
40	036-074-372	f	2001	275.1	75.6	9.61865	20.09034	15.53129	3.465454
41	036-053-256	f	2001	452.15	82.7	12.02865	48.16467	38.75744	12.86432
41	036-053-256	f	2003	365.675	86.7	1.6807	8.515997	6.5077	1.814778
41	036-053-256	f	2004	515.57	86.3	2.75555	3.90149	3.135498	0.901482
42	036-045-772	f	2003	445.56	82.6	4.9376	8.515997	6.5077	1.814778
43	036-044-527	f	2003	338.8	78.4	10.6762	8.84891	6.946911	1.886008
43	036-044-527	f	2004	320.63	78.7	12.22065	3.463666	2.61161	0.603032
44	036-044-780	m	2001	346.8	74.3	11.2376	25.34599	20.05593	5.809787
45	035-880-783	m	2008	690.22	86.4	37.27955	102.9501	81.99762	27.15993
45	035-880-783	m	2009	611.02	87.9	18.7007	34.15828	27.87561	8.653455
47	035-877-827	m	2006	995.47	104.6	23.09325	233.2384	187.756	64.94947
51	027-088-338	m	2006	1017.45	104.1	29.6026	4.923997	3.738221	0.815986
52	027-011-573	f	2001	376.1	79.8	33.656	19.17629	15.37612	4.952475
52	027-011-573	f	2002	412.61	80.4	9.18075	25.6858	20.37075	6.667303
52	027-011-573	f	2004	359.12	81.4	4.6715	14.69557	11.6667	3.329517
53	027-012-858	f	2001	331.4	73.9	11.5793	8.507579	6.559427	1.631539
53	027-012-858	f	2002	396.58	72.8	2.3998	7.159384	5.625395	1.743405
53	027-012-858	f	2004	319.18	75.1	8.11495	17.72768	14.58093	5.371013
54	027-019-278	m	2000	1373	104.1	16.85555	31.98622	24.67695	6.814178
55	027-035-769	m	2005	336.94	79.6	7.21675	2.175274	1.659683	0.415685
57	026-890-627	f	2000	528	88.8	3.4258	6.760708	5.341111	1.586054
57	026-890-627	f	2002	662	91.9	3.09105	1.433369	1.12312	0.338818
58	025-791-553	f	2000	355	77.1	9.03905	9.046554	6.953567	1.507609
58	025-791-553	f	2001	411	77.5	7.61705	13.68003	10.86347	2.956163
58	025-791-553	f	2002	363.82	74.1	19.93295	3.096224	2.408415	0.661906
59	025-595-308	m	2001	415.2	81.3	24.20515	53.77587	42.11691	10.98409
60	025-328-281	m	2001	786.8	93.9	20.5106	43.1871	35.29789	11.66364
60	025-328-281	m	2002	855.5	98.1	54.9812	52.07747	39.85717	11.35479
60	025-328-281	m	2003	1185.17	101.3	7.7633	6.039386	4.786355	1.227553

61	025-305-540	f	2005	606.13	90.7	13.34625	22.69852	18.0112	5.285986
62	025-267-096	f	2000	443	88.2	1.80025	3.688578	3.04867	1.057892
62	025-267-096	f	2001	388.1	88.9	4.6845	11.52282	9.006208	2.188021
62	025-267-096	f	2003	442.45	89.1	4.223	3.182787	2.441019	0.629014
62	025-267-096	f	2004	394.47	87.2	3.76705	2.003258	1.530264	0.309523
63	024-308-878	f	2000	448	84.1	4.03845	12.29478	9.999906	3.316474
63	024-308-878	f	2001	497.4	86	5.88265	6.450475	4.934348	1.246932
63	024-308-878	f	2002	470.31	85.6	6.8053	0.846375	0.621743	0.131882
63	024-308-878	f	2004	463.39	86.2	14.7996	1.274535	0.963258	0.201289
63	024-308-878	f	2005	440.57	85.4	3.4288	2.041563	1.580661	0.386986
63	024-308-878	f	2008	395.19	86.7	3.71425	3.210714	2.457665	0.550863
64	024-275-523	m	2000	499.5	88.1	23.25765	6.417376	4.976915	1.214794
65	023-367-888	f	2005	583.82	90.6	5.2757	15.74804	12.57073	4.087284
65	023-367-888	f	2006	548.64	92.2	4.8961	9.005839	7.219341	2.178174
65	023-367-888	f	2007	512.3	90.2	5.50005	8.676572	6.995295	2.318213
65	023-367-888	f	2009	501.63	91.8	6.2538	17.18861	14.08973	4.854201
65	023-367-888	f	2010	488.35	87.7	3.2641	8.413715	6.835602	2.218163
66	023-342-795	m	2002	1419.83	106.2	74.23035	122.1879	97.08725	25.71103
67	019-527-635	m	2001	891.1	99.1	77.3684	99.33362	77.68695	19.20155
68	017-771-311	f	2001	545.3	80.5	3.6153	6.885333	5.554948	1.527762
68	017-771-311	f	2002	769.6	84.8	5.1883	13.20006	10.3334	3.057593
69	016-059-111	f	2002	499.84	83.4	11.041	2.457257	1.892106	0.424083
69	016-059-111	f	2003	522.69	83.4	5.0755	4.839281	3.941824	1.24136
69	016-059-111	f	2004	625.51	83.1	3.3088	0.738963	0.551568	0.098587
69	016-059-111	f	2005	414.1	84.3	22.2589	8.018812	6.316567	1.591191
69	016-059-111	f	2006	370.41	83.7	9.24545	6.263516	4.705329	0.847658
70	017-602-115	m	2000	373	76.1	12.5208	24.72061	19.50091	4.526889