

**HOME RANGE SIZE AND HABITAT SELECTION OF  
TIMBER RATTLESNAKES (*CROTALUS HORRIDUS*)  
IN SOUTHWESTERN WISCONSIN**

By

Christopher M. Hamilton

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APPROVED BY THE GRADUATE COMMITTEE OF

---

Dr. Kevin R. Russell, Committee Chairman  
Associate Professor of Wildlife Ecology and Management  
College of Natural Resources

---

Dr. Michael J. Hansen  
Professor of Water Resources and Fisheries  
College of Natural Resources

---

Dr. Tim F. Ginnett  
Associate Professor of Wildlife Ecology and Management  
College of Natural Resources

## ABSTRACT

The timber rattlesnake (*Crotalus horridus*) has experienced rangewide declines at least partially as a result of human exploitation and persecution, is listed as a threatened species in at least 9 states, and has received “protected wild animal” status in Wisconsin. While some persecution persists, current impacts on the species are thought to be largely associated with habitat alteration, including human development and vegetative succession. Knowledge of home range size and habitat selection is essential to conservation of timber rattlesnakes in Wisconsin, which are now experiencing increased conversion of critical habitats for residential use. However, the ecology of this species in the Upper Mississippi region is poorly understood. My objectives were to determine if home range size or habitat selection of timber rattlesnakes (1) differed among groups of males, non-gravid females and gravid females and (2) between protected natural areas and a residential development.

I used radio telemetry to track 36 timber rattlesnakes in southwestern Wisconsin during 2007 and 2008. I generated minimum-convex polygon home ranges for 34 of the snakes, which were tracked for periods of 11 to 20 weeks between May and October of each year. I used factorial analyses of variance (ANOVA) to compare total distance moved (TD), average daily distance moved (ADD), and home range area (HR) among male, non-gravid female, and gravid female rattlesnakes and between two protected natural areas and a residential development. Mean movement did not differ significantly between males (TD: 2981 m [95% CI 2238.8 to 3968.3 m]; ADD: 27.7 m [95% CI 21.0 to 36.5 m]; HR: 21.1 ha [95% CI 11.4 to 39.0 ha]) and non-gravid females (TD: 2082 m [95% CI 1520 to 2851 m]; ADD: 21.8 m [95% CI 16.1 to 29.5 m]; HR: 13.3 ha [95% CI

6.7 to 26.1 ha]). However, movement of gravid females (TD: 483 m [95% CI 351 to 663 m]; ADD: 4.9 m [95% CI 3.6 to 6.6 m]; HR: 0.7 ha [95% CI 0.3 to 1.3 ha]) was significantly smaller ( $p < 0.001$  for all parameters) than for males or females. Movement and activity of rattlesnakes did not differ significantly between sites. The size of male timber rattlesnake home ranges was positively related to snake length ( $R^2 = 0.73$ ,  $p < 0.001$ ) but not for either gravid ( $R^2 = 0.01$ ,  $p = 0.815$ ) or non-gravid females ( $R^2 = 0.21$ ,  $p = 0.157$ ).

I used both discriminant function analysis (DFA) and logistic regression with Akaike's Information Criterion (AIC) model selection to model timber rattlesnake habitat selection based on 8 habitat variables. Variables were measured at locations used by snakes ( $n = 523$ ) and random locations assumed to be available to the snakes ( $n = 519$ ). Measurements from locations were averaged for each snake to create vectors of snake habitat use ( $n = 36$ ) and habitat available to snakes ( $n = 36$ ) for analysis. The first two discriminant functions identified percent cover of rock, presence of brush piles, and tree stem density as the most important habitat features associated with rattlesnake habitat use. This DFA model was similar to the best approximating logistic regression model identified from AIC model selection. The third discriminant function in the DFA model included relative predominance of eastern redcedar (*Juniperus virginiana*) as an important habitat feature at sites used by timber rattlesnakes, as did the second-best supporting model from logistic regression ( $\Delta AIC_c = 1.11$ ). Habitat selection of timber rattlesnakes was also influenced by reproductive status. Gravid females used areas with relatively high amounts of rock. Males and non-gravid females used areas of higher tree density and brush piles, particularly in the developed area. Habitat use by gravid females

also differed between sites, with snakes in the residential development using areas with higher relative dominance of eastern redcedar than snakes in the natural area treatment, presumably because rocky areas without eastern redcedar were scarce in the developed area.

Home ranges and habitat selection of timber rattlesnakes in southwestern Wisconsin vary as a function of both sex and reproductive status. Therefore, management strategies designed to conserve this species in the region should reflect these gender- and reproduction-related differences. Gravid females are relatively stationary, and small patches of habitat should be suitable as long as the requisite features of surface rock and open forest canopies are present. Males, however, range widely and their home ranges encompass a broader array of habitat features. Therefore, conservation of males will require broader-scale conservation measures with a focus on minimizing mortality on roads and direct human-rattlesnake conflicts. Inclusion of movement corridors in residential developments with strategic placement of brush piles may facilitate timber rattlesnake movements while minimizing risks to humans.

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## INTRODUCTION

The timber rattlesnake (*Crotalus horridus*) ranges widely in the eastern third of North America from southern New Hampshire and southern Ontario to northern Georgia and west to southeastern Minnesota through northeastern Texas (Fig. 1; Vogt 1981; Brown 1993) but has been extirpated from portions of its historic range, including Maine and Rhode Island. In Wisconsin, timber rattlesnakes are currently restricted to the southwestern corner of the state along the Mississippi River and Wisconsin River corridors, although historically the species was more widespread (Oldfield and Keyler 1989). Timber rattlesnake populations in Wisconsin declined as a result of bounty-hunting that began in the 1920s and continued until 1975. The impacts of bounties on timber rattlesnake populations were severe in Wisconsin (WDNR 2006) and similar to those in New York and Minnesota (Brown 1993). Eradication efforts were particularly successful in Wisconsin and other northern states because of the tendency of gravid females to remain congregated near hibernacula where they were killed at disproportionately high rates.

Although the historic boundary of the species' range appears relatively stable, current populations of timber rattlesnakes within this range are increasingly fragmented and isolated and has undergone extensive population declines as a result of habitat alteration, collection, and human persecution (Brown 1993). Timber rattlesnakes are considered rare to imperiled in 16 states, have been designated as endangered or threatened in 13 of those states, and have been extirpated from 2 others (Brown 1993). In 1997, the timber rattlesnake was proposed for listing as a threatened species in the state

of Wisconsin. The proposed listing failed, but the species was designated as a “protected wild animal” in 1998, which made possession or hunting illegal in Wisconsin.

Timber rattlesnakes in Wisconsin and Minnesota are generally found in bluff woodlands and prairies along the Mississippi and Wisconsin Rivers, where topography and limestone geology are favorable for den sites (Schorger 1968; Vogt 1981; Oldfield and Keyler 1989). These hibernacula, typically rock fissures and crevices along bluffs, are necessary for winter survival (Brown et al. 2007). In late April to early May, timber rattlesnakes begin to emerge from hibernacula and occupy rocky outcrops and other forest openings with southerly exposures. Similar habitats are used in late summer and early autumn prior to re-entering dens in October (Sajdak and Berg 2005). During summer, non-reproductive adults disperse into adjacent deciduous forests and open valleys, whereas gravid females remain near hibernacula where they bask on relatively open bluff prairies (Sajdak and Berg 2005). As with most snakes, habitat requirements of juvenile timber rattlesnakes are poorly understood (Gregory et al. 1987; Reinert 1993).

The habitat ecology of timber rattlesnakes has been widely studied in the eastern United States (e.g., Galligan and Dunson 1979; Reinert 1984a, b; Martin 1992, 1993; Waldron et al. 2006; Brown et al. 2007). Minimum convex polygon home range sizes of timber rattlesnakes range from 1.8 ha for gravid females to 123 ha for adult males (Reinert and Zappalorti 1988a; Waldron et al. 2006). Timber rattlesnakes select habitat based on reproductive status, with gravid females selecting more open, rocky habitats than either males or non-gravid females (Reinert 1984a, b). In Wisconsin, however, information on timber rattlesnake habitat ecology is limited to general habitat associations (Sajdak and Berg 2005), brief descriptions of habitat used by gravid females

(Keenlyne 1972, 1978), and unpublished reports (R.A. Sajdak 1999, 2000; R.A. Sajdak and A. Bartz 2001).

Urbanization and habitat fragmentation are increasingly viewed as major threats to wildlife populations (Czech et al. 2000; Johnson 2001; Sanderson et al. 2002; Groom et al. 2006). Reptiles and amphibians are no exception to this pattern (Dodd 1987, 1993; Mitchell and Jung Brown 2008). Low-density development in rural areas is the fastest-growing form of land use in the United States, and is particularly widespread in amenity-rich regions of the eastern United States (Hammer et al. 2002; Brown et al. 2005; Hansen et al. 2005; Radeloff et al. 2005). Land located along bluffs overlooking the Upper Mississippi River, for example, has been increasingly developed in recent years.

Although direct mortality from human persecution and exploitation (e.g., skins) largely contributed to historic population declines of timber rattlesnakes (Galligan and Dunson 1979; Brown 1993), habitat loss from increasing residential development combined with changes in forest cover and structure (e.g., succession of forest openings) within bluff habitats of southwestern Wisconsin are currently considered the primary threats to the species (Brown 1993; WDNR 2005, 2006). Therefore, thorough knowledge of activity patterns, home-range characteristics, habitat requirements of timber rattlesnakes, and potential effects of land use practices are essential for effective conservation of timber rattlesnakes (Dodd 1993; Roe et al. 2003).

My first objective was to determine if home range sizes of timber rattlesnakes in southwestern Wisconsin differed as a function of sex, reproductive status, or bluff disturbance. I used radio telemetry to monitor locations of 34 timber rattlesnakes in 2007 and 2008. I determined if rattlesnake home ranges differed between 1) males and

females, 2) non-gravid and gravid females, and 3) disturbed and protected habitats. In addition, I used linear regression to determine if home range area was dependent on age.

My second objective was to determine if habitat selection of timber rattlesnakes differed as a function of sex, reproductive status, or bluff disturbance. To accomplish this objective, I used discriminant function analysis (DFA; McGarigal et al. 2000) and logistic regression with Akaike's information criterion (AIC; Burnham and Anderson 2002) model selection to evaluate which habitat variables differentiated between used and random locations for individual snakes. Finally, I determined if model variables that explained locations selected by timber rattlesnakes differed between 1) males and females, 2) non-gravid and gravid females, and 3) disturbed and protected habitats.

## **MATERIALS AND METHODS**

### **Study area**

I conducted my study at three sites in Vernon and Crawford counties, Wisconsin (Fig. 2). The first site was Rush Creek State Natural Area, a 2,024-ha natural area established and managed by WDNR to maintain remnant bluff prairie and oak (*Quercus* spp.) woodland communities. The second site was 10 km north of Rush Creek in Battle Hollow, a portion of the Battle Bluff State Natural Area that also was established for bluff prairie and oak woodland management. The third site, near the town of De Soto, Wisconsin was in an area that has undergone extensive residential development. I focused my sampling efforts on six major hibernacula within the study area (Rush Creek SNA = 2, Battle Hollow SNA = 1, De Soto = 3) that were separated by 0.5-6 km, although these dens may actually exist as complexes of smaller groups of hibernating snakes (R.A. Sajdak, personal communication).

The study area is located within the North-Central U.S. Driftless and Escarpment section (“Driftless Area”) of the Eastern Broadleaf Forest physiographic province (McNab and Avers 1994). The climate is continental with precipitation ranging from 2.5 to 11.1 cm per month, mostly as rainfall between April and August. The mean annual temperature is 9°C and ranges from 23.5°C in July to -8.2°C in January (NOAA 2008). Elevation within the study area ranges from 250 to 400 m and topography consists of dissected, upland plateaus with steep bedrock ridges descending to river drainages that ultimately flow to the Mississippi River. Soils are predominantly sand and silt loams over dolomite and sandstone (WDNR 2005).

Forests of the Driftless Area were historically a transition zone between forest and grassland. Before European settlement, the area was covered by an oak savanna complex of mixed grasslands with upland forests of sugar maple (*Acer saccharum*) and basswood (*Tilia americana*) and riverine forests of elm (*Ulmus* spp.), ash (*Fraxinus* spp.), and cottonwood (*Populus deltoides*; Curtis 1959). These oak savannas, under fire suppression and modern agricultural practices, succeeded to closed-canopy (50-95%) oak-hickory (*Carya* spp.) woodlands within a matrix of row and forage crops (Leach and Givnish 1999). Predominant oak species included white oak (*Q. alba*), red oak (*Q. rubra*), black oak (*Q. velutina*), and bur oak (*Q. macrocarpa*). Although oak-hickory was the predominant cover type, many stands included a mix of hardwood species including cherry (*Prunus serotina*), slippery elm (*U. rubra*), basswood, sugar maple, white ash (*F. americana*) and black walnut (*Juglans nigra*). Many forest stands in the area were between 50 and 70 years old.

Most woodlands in the study area were on steep slopes adjacent to streams that formed a connected, dendritic pattern. Scattered remnant prairie openings existed in the study area, particularly on the bluffs near the Mississippi River. Habitats immediately surrounding hibernacula were typically prairie remnants dominated by grasses and forbs. In many areas, openings were invaded by eastern redcedar (*Juniperus virginiana*) because of fire suppression. Complex topography and erosive soils in the driftless area support less intensive agriculture than in many parts of the Midwest, with agriculture replacing grasslands over 30–40% of the landscape (McNab and Avers 1994). Residential development is increasingly common along the Mississippi River bluffs.

### **Radiotelemetry**

I captured 36 timber rattlesnakes for this study between April and June of 2007 and 2008 as they dispersed from hibernacula. Snakes were captured using a hook and reptile sack (Fitch 1987). I recorded the mass of each snake with a Pesola scale. Snakes were then placed in a “squeeze box” (Cross 2000) to allow safe determination of gender and measurement of morphological attributes (Ivanyi and Altimari 2004). Gender of snakes was determined by probing for the presence of hemipenes (Schaefer 1934; Fitch 1987). I measured total length (TL) of snakes in the squeeze box by tracing a line down the center of the dorsum (Bertram and Larsen 2004). I then gently pulled the tail of the snake through a hole in the squeeze box to measure length from the anal plate to tail tip. Snout-vent length (SVL) of snakes was estimated by subtracting tail length from total length (Bertram and Larsen 2004).

After capture and measurement, snakes were transported in aquaria to the University of Wisconsin - Madison School of Veterinary Medicine where radio



transmitters (SI-2, 13 g, Holohil Systems, Carp, ON, Canada) were implanted following procedures outlined by Reinert and Cundall (1982). Transmitters were less than 5% of snake body weight. Snakes were also marked with Passive Integrated Transponder (PIT) tags for individual recognition in case of transmitter failure. Following surgery, snakes were monitored for 2-3 days before being released at their capture locations. Capture, handling, and surgical protocols followed venomous reptile Institutional Animal Care and Use Committee (IACUC) guidelines (Anderson and Talcott 2006) approved by the University of Wisconsin – Stevens Point IACUC (#200710.01).

Radio-tagged timber rattlesnakes were monitored between May and October in 2007 and 2008 using standard telemetry procedures (White and Garrott 1990; Reinert 1992). I used ATS-410 and ATS-2000 receivers (Advanced Telemetry Systems Inc., Isanti, MN USA) and hand-held, three-element Yagi antennas to measure point locations for each individual by homing in on snakes (White and Garrott 1990; Reinert 1992). I recorded the site of visual observations with a Global Positioning System unit (GPS; Garmin International Inc., Olathe, KS, USA). Locations were recorded at the moment of visual sighting to reduce error associated with animal disturbance and movement (White and Garrott 1990). I attempted to locate each snake 1-2 times per week. Consecutive radio locations from individual snakes were separated by  $\geq 3$  days to reduce spatial autocorrelation (Swihart and Slade 1985). I consider 3 to 7 days adequate because multiple snakes were observed traversing their entire home range in three days during the course of the study. I varied time of day for locations (restricted to daylight hours) to avoid temporal autocorrelation. Location data for all snakes included movements to or from known hibernacula within natural areas and the residential development.

## **Home ranges, activity, and movements**

I estimated total distance moved (TD), average daily distance moved (ADD), and home range area (HR) of 34 timber rattlesnakes with ArcGIS 9.3 (ESRI, Redlands, California, USA) using the minimum convex polygon (MCP) estimator in the Hawth's Analysis Tools for ArcGIS add-in (Hawth's Tools; Beyer 2004). A minimum of 14 locations was used to estimate individual activity variables. Two snakes with 7 and 11 locations were not included in home range analyses. Total distance moved was calculated by summing linear distances between successive snake locations. Average daily distance moved was calculated by dividing total distance moved by total tracking period. Fixed kernel estimators are often considered superior to MCP for home range analysis (Worton 1989), but have been criticized as overestimating home ranges of herpetofauna (Row and Blouin-Demers 2006). Therefore, I used the MCP method to estimate home range, which also facilitates comparison to previous studies of timber rattlesnake home range (Fitch and Shirer 1971; Reinert and Zappalorti 1988a; Laidig and Golden 2004; Adams 2005).

I used factorial analysis of variance (ANOVA; Zar 1984) to determine if total distance moved, average daily distance moved, or home range size of timber rattlesnakes differed among groups (males, non-gravid females, gravid females) or between study sites (natural and disturbed). I also divided the active season (May-October) into five periods and compared average daily distance moved among groups, periods, and sites using factorial ANOVA. This allowed me to test for potential group by site interactions. I used Tukey's honestly significant difference (HSD) to identify groups that differed. Home range and movement data were log-transformed to ensure homogeneity of variance

among groups as indicated by Levene's test. In addition, I calculated Pearson's correlation coefficients to determine whether activity variables were related to total number of days tracked or total number of locations used to determine home ranges. Finally, to compare my results with other studies, I used ANOVA on log-transformed MCP home range area estimates from a timber rattlesnake study from the New Jersey pine barrens (Reinert and Zappalorti 1988a). I first conducted a one-way ANOVA of home range area for male, non-gravid female, and gravid female timber rattlesnakes using just the New Jersey data. I then used factorial ANOVA to determine if home range or activity parameters differed among groups or between studies using data from my study and Reinert and Zappalorti (1988a).

I used linear regression to determine if there was a relationship between home range area and snake snout-vent length to evaluate potential age-related influences on home range size. I used snake length as a surrogate for age because snake age was not known. I assumed that, on average, older snakes were longer than younger snakes (Heyrend and Call 1951). I pooled data across sites and analyzed male, non-gravid female, and gravid female snakes separately. SPSS 16.0 (SPSS, Inc., Chicago, IL, USA) was used for all statistical analyses and the significance level for all tests was  $\alpha = 0.05$ .

Lastly, I examined a subset of snake home ranges ( $n = 6$ ) for overlap by measuring static territorial interaction. Further analyses were not conducted because the number of snakes tracked varied widely among groups and den sites for each year. In static territorial interaction, the home range areas of 2 animals ( $A_1$  and  $A_2$ , respectively) and the area of home range overlap ( $A_{1,2}$ ) is measured. The static interaction ( $S$ ) is given by:

$$S_{1,2} = A_{1,2}/A_1$$

and

$$S_{2,1} = A_{1,2}/A_2$$

where  $S_{1,2}$  is the proportion of animal 1's home range shared with animal 2 and  $S_{2,1}$  the proportion of animal 2's home range shared with animal 1 (White and Garrott 1990).

The static interactions will not be equal unless the home range areas of the two animals are equal.

### **Habitat Selection**

Habitat characteristics in home ranges of all 36 timber rattlesnakes tracked during 2007-2008 were measured during June through mid-September of each year. I used ArcGIS 9.3 (ESRI, Redlands, California, USA) and the Hawth's Tools add-in to develop a minimum convex polygon (MCP) home range for each snake in mid-August of each year, at which time the snakes had reached the furthest extent of their home ranges and subsequent movements were associated with a slow return to their hibernacula. I then used the Hawth's Tools random point generator to generate random habitat sampling locations within each MCP. These random locations were assumed to be available to an individual rattlesnake within its home range (Manly et al. 2002).

At each used and random location, I measured 20 habitat variables (Table 1) that were predictive of timber rattlesnake presence based on my own observations or because they were previously identified as important to timber rattlesnake use (e.g., Reinert 1984a, b, 1993; Waldron et al. 2006; Luiselli et al. 2007). I estimated average overhead canopy cover at each location from a spherical densiometer readings in each cardinal direction (Lemmon 1956). I used the point-centered quarter method (Cottam and Curtis

1956; Beasom and Haucke 1975) to estimate species composition, size, and density of overstory trees at each location. At each location, the species, diameter at breast height (dbh; cm), and distance (m) to nearest  $\geq 7.5$ -cm tree in each quarter was measured. The distance to (m) and diameter (cm) of the downed log nearest to each location was measured. Within a 1-m<sup>2</sup> quadrat centered on each location (Reinert 1984a, b), I visually estimated the percent (%) cover of exposed rock, leaf litter, herbaceous vegetation, eastern redcedar, and downed wood. The length (cm) of the largest encroaching rock, number of woody stems, and height (cm) of the tallest woody stem were measured within each quadrat. I created binary response variables to assess presence or absence of herbs, vines, shrubs (<7.5 cm dbh and <2 m height), brush/wood piles, and ground juniper (*Juniperus communis*) within each quadrat. I defined “present” to be >20% cover within the square meter centered on the snake. I selected >20% cover because it is sufficient to conceal a large, coiled timber rattlesnake.

### **Habitat Selection Analysis**

I used linear discriminant function analysis (DFA; McGarigal et al. 2000) and logistic regression with Akaike’s Information Criterion (AIC) model selection (Burnham and Anderson 2002) to determine which habitat variables were most useful for differentiating between used and available (i.e., random) locations. Available locations were pooled for DFA analysis and were compared within individual timber rattlesnake home ranges for the logistic regression analysis (Type II and III habitat selection studies, respectively; Manly et al. 2002). I used DFA as my primary modeling approach because it is frequently used to model habitat selection (McGarigal et al. 2000) and is directly comparable to previous studies of timber rattlesnake habitat use (e.g., Reinert 1984a, b,

1993). I also used logistic regression with AIC model selection because it has less stringent assumptions and because different multivariate techniques applied to the same data (e.g., known and random locations) may identify distinctly different suites of explanatory variables (Rexstad et al. 1988). Further, although logistic regression is widely used for examining patterns of species occupancy (O'Connor 2002), *a priori* model specification and information-theoretic model selection have recently been criticized (Guthery et al. 2005). The analyses were performed using SPSS for Windows version 16.0 (SPSS, Inc., Chicago, IL, USA).

*Discriminant function analysis*— DFA generates linear combinations of variables that partition data along orthogonal axes in canonical space to maximize separation of pre-identified groups (e.g., used and random locations). I averaged habitat variable measurements for all locations of each snake to create a total of 38 vectors (1 for each snake and 1 each for random locations in the developed and natural sites), because using each individual location in the analyses would constitute pseudoreplication (Hurlbert 1984). Averaging measurements of habitat variables had the additional benefit of converting binary variables into proportions of occurrence for subsequent analyses. Then I used multivariate analysis of variance (MANOVA) to determine if habitat centroids differed significantly among groups (males, non-gravid females, gravid females, random locations, sites) and then used DFA to determine axes along which groups differed and which habitat variables contributed to group differences among used and random locations (Reinert and Zappalorti 1988a; Blouin-Demers and Weatherhead 2001a). Prior to analysis, I eliminated redundant variables using a Pearson's correlation coefficient matrix ( $r$ ):

$$r = \frac{SS_{XY}}{\sqrt{(SS_X)(SS_Y)}} = \frac{\sum_{i=1}^n (X_i - \bar{X})(Y_i - \bar{Y})}{\sqrt{\sum_{i=1}^n (X_i - \bar{X})^2 \sum_{i=1}^n (Y_i - \bar{Y})^2}}$$

where  $SS_{XY}$  is the sum of crossproducts and  $SS_X$  and  $SS_Y$  are the sum of squares for variables  $X$  and  $Y$ , respectively. When Pearson's  $r$  was  $\geq 0.60$  for a pair of variables, I removed the variable with the lowest p-value in a one-way ANOVA among groups. Most of the original 20 variables were either highly correlated, used to create composite variables, or were determined to not contain meaningful information, thereby resulting in 8 variables retained for analysis (Table 2). Categorical variables were transformed into dummy variables (Cohen and Cohen 1983). Variables were assessed for normality using Kolmogorov-Smirnov tests ( $P < 0.05$ ). Where necessary, variables were log- or arcsin-transformed to better meet the assumption of normality. However, DFA is robust to non-normally distributed data with large samples (e.g.,  $n > 100$ ; Tabachnick and Fidell 1996). I used Box's M-test to test for equality of population covariance matrices (McGarigal et al. 2000). I conducted DFA classification using group covariance matrices of the canonical discriminant functions because covariance matrices departed significantly from equality (Tabachnick and Fidell 1996). At each step of the forward stepwise DFA, the variable that minimized the overall Wilks'  $\lambda$  with a  $P$ -value of  $\leq 0.05$  was entered. I used the model Wilks'  $\lambda$  value to evaluate statistical significance and determined relative importance of habitat variables by examining the magnitude of the standardized canonical correlation coefficients.

*Logistic regression*— I averaged all locations to create 72 vectors for logistic regression, 1 for the used and random locations of each snake. Prior to model

development, I eliminated redundant variables (Pearson's  $r \geq 0.60$ ) and examined scatter plots and residual plots to ensure that measurements did not contain presumed outliers ( $>4$  SD). I then specified a set of *a priori* candidate logistic regression models (Burnham and Anderson 2002):

$$Y = \frac{e^{(\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n)}}{1 + e^{(\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n)}}$$

where  $e$  is the base of the natural logarithm and  $X_n$  and  $\beta_n$  are variables and their associated coefficients. Model specification was based on (1) a review of published literature on habitat selection by timber rattlesnakes and (2) my experience with this species. Because preliminary analyses revealed that male and non-gravid female snakes responded similarly to habitat variables, I pooled them as “non-gravid” within each site treatment before conducting my final analyses. I specified a global model containing 9 variables (Table 3). This included two dummy variable for reproductive status and study area called “non-gravid” and “site. My proposed model set included the global model and two sets of 23 models, for a total of 47 nested models representing potential influences of habitat and snake attributes on rattlesnake habitat selection (Table 4). The second set of 23 models mirrored the first but included a variable for “site”. Male/non-gravid female and the natural area site were references for the dummy variables (Table 3). I did not consider all possible combinations of variables, because this typically inflates the number of models beyond what can be practically analyzed (Burnham and Anderson 2002).

I used Akaike's Information Criterion (AIC; Hurvich and Tsai 1989; Burnham and Anderson 2002) for model selection:



$$AIC = -2\log[L(\hat{\theta}|data)] + 2K$$

where  $\log[L(\hat{\theta}|data)]$  is the likelihood of the estimated model parameter ( $\hat{\theta}$ ) given the data and  $K$  is the number of parameters in the model. Others (e.g., Boyce et al. 2002) have suggested that this method is appropriate to select the best model from a set of alternative models derived from use versus availability data. Because the number of snakes ( $n$ ) was small relative to the number of variables ( $K$ ) included in some models (i.e.,  $n/K < 40$ ), I used  $AIC$  corrected for small sample size ( $AIC_c$ ; Burnham and Anderson 2002).

$$AIC_c = AIC + [(2K(K+1))/(n-K-1)]$$

I ranked candidate models according to their  $AIC_c$  values and the best model (i.e., most parsimonious, designated  $AIC_{min}$ ) is the model with the smallest  $AIC_c$  value (Burnham and Anderson 2002). I drew primary inference from models within 2 units of  $AIC_{min}$ , although models within 4-7 units may have limited empirical support (Burnham and Anderson 2002). I calculated Akaike weights ( $w_i$ ) to determine the weight of evidence in favor of each model (Burnham and Anderson 2002) using:

$$w_i = e^{(-0.5\Delta_i)} / \sum_{r=1}^R e^{(-0.5\Delta_r)}$$

where  $e$  is the base of the natural logarithm,  $i$  = the  $i^{\text{th}}$  model of the set of candidate models,  $\Delta_i$  is the difference between the  $i^{\text{th}}$  model ( $AIC_i$ ) and the model with the lowest AIC value ( $AIC_{min}$ ) and  $r = 1$  to  $R$  is the full set of candidate models evaluated. This procedure normalizes the model likelihoods so that individual model weights ( $w_i$ ) are a relative proportion of the summed model weight. To assess model fit of supported models, I calculated Nagelkerke's rescaled  $R^2$ . All categorical variables were

transformed into dummy variables (Cohen and Cohen 1983) and coefficients were calculated relative to the most frequently occurring category for each variable.

## RESULTS

### Radiotelemetry

Between May 2007 and October 2008, I measured locations of 36 timber rattlesnakes within two protected natural areas ( $n = 18$ ) and a residential development ( $n = 18$ ). Individual snakes were tracked for periods ranging from 75 to 150 days, and the number of locations per snake ranged from 7 to 22 in a given year.

### Home ranges, activity, and movements

I used 13 male, 11 non-gravid female, and 10 gravid female snakes to estimate home range and activity (Table 5). Male timber rattlesnakes moved the largest total distances, average daily distances moved, and had the largest home ranges, with gravid females exhibiting the smallest and non-gravid females exhibiting intermediate values for all parameters (Table 6; Figs. 3 and 4). Total distance, average daily distance, and home range area did not significantly differ between sites (TD:  $F_{1,28} = 0.429$ ,  $p = 0.518$ ; ADD:  $F_{1,28} = 0.341$ ,  $p = 0.564$ ; HR:  $F_{1,28} = 0.319$ ,  $p = 0.577$ ). However, total distance, average daily distance, and home range area were significantly different for snakes of different sex or reproductive status (TD:  $F_{2,28} = 41.108$ ,  $p < 0.001$ ; ADD:  $F_{2,28} = 41.524$ ,  $p < 0.001$ ; HR:  $F_{2,28} = 32.880$ ,  $p < 0.001$ ). Tukey's HSD test indicated that gravid females exhibited significantly smaller values for total distances moved, average daily distances moved, and home range sizes than either males or non-gravid females ( $p < 0.001$  for all

parameters). However, Tukey's HSD test indicated that movement did not differ significantly between males and non-gravid females (TD:  $p = 0.198$ ; ADD:  $p = 0.475$ ; HR:  $p = 0.555$ ) (Table 6, Figs. 4 and 5). No significant site-by-sex or reproductive status interactions occurred (TD:  $F_{2, 28} = 1.555$ ,  $p = 0.229$ ; ADD:  $F_{2, 28} = 1.590$ ,  $p = 0.222$ ; HR:  $F_{2, 28} = 1.022$ ,  $p = 0.373$ ) (Table 6, Figs. 4 and 5).

Average daily distance moved during tracking periods differed significantly by sex ( $F_{2, 575} = 68.208$ ;  $p < 0.001$ ) and by tracking period ( $F_{4, 575} = 2.922$ ;  $p = 0.021$ ). Tukey's HSD test indicated that gravid female timber rattlesnakes moved shorter average daily distances than both males and non-gravid females ( $p < 0.001$ ) but that there was no difference between males and non-gravid females ( $p = 0.153$ ). While the ANOVA indicated a difference among tracking periods, Tukey's HSD test indicated that there were no differences among tracking periods. The lowest p-value given was for the comparison between the second and third tracking period ( $p = 0.058$ ). In addition, the factorial ANOVA revealed a significant sex-by-tracking period interaction for average daily distance moved ( $F_{8, 575} = 2.164$ ,  $p = 0.029$ ) (Fig. 5). Confidence intervals indicated that gravid females moved greater daily distances during the tracking period immediately following emergence from the den than during the rest of the season, male movement distances increased between the second and third tracking period, and non-gravid females moved similar distances throughout the season (Fig.5).

Home range area did not differ significantly among male, non-gravid female, and gravid female timber rattlesnakes from the pine barrens of New Jersey ( $F_{2, 16} = 2.943$ ,  $p = 0.082$ ). Home range area differed significantly between studies (HR:  $F_{1, 47} = 6.609$ ,  $p = 0.013$ ) but total distance and average daily distance moved did not significantly differ

(TD:  $F_{1,47} = 1.384, p = 0.245$ ; ADD:  $F_{1,47} = 0.219, p = 0.642$ ). Total distance moved, average daily distance moved, and home range area differed significantly among male, non-gravid female, and gravid female timber rattlesnakes (TD:  $F_{2,47} = 24.994, p < 0.001$ ; ADD:  $F_{2,47} = 26.679, p < 0.001$ ) (Figs. 6a-c). Tukey's HSD test indicated that gravid female timber rattlesnakes were significantly different from both males and non-gravid females for all parameters (TD:  $p < 0.001$ ; ADD:  $p < 0.001$ ; HR:  $p < 0.001$ ) but that there was no difference between males and non-gravid females (TD:  $p = 0.193$ ; ADD:  $p = 0.280$ ; HR:  $p = 0.286$ ). In addition, the factorial ANOVA revealed an interaction between study site and sex or reproductive status for total distance moved, average daily distance moved, and home range area (TD:  $F_{2,47} = 6.441, p = 0.003$ ; ADD:  $F_{2,47} = 7.900, p = 0.001$ ; HR:  $F_{2,47} = 5.716, p = 0.006$ ) (Fig. 6 a-c). Gravid female total distance moved, average daily distance moved, and home range area values were significantly smaller in Wisconsin than in New Jersey but there were no differences between males and non-gravid females from the two study sites (Figs. 6 a-c).

Home range overlap between snakes ranged from 0 to 0.9, with up to 5 snakes sharing the same area of forest (Table 7, Fig. 7). Snake home ranges from this den included 5 males and 1 non-gravid female.

Total distance moved, average daily distance moved and home range area were not correlated to either number of days tracked or number of locations used in analyses for male and non-gravid female snakes. However, the total number of days tracked was correlated to total distance moved for gravid females ( $r = 0.635, p = 0.049$ ).

Snout-vent length was not related to home range area for either gravid females ( $R^2 = 0.007, p = 0.815$ ) or non-gravid females ( $R^2 = 0.210, p = 0.157$ ) (Figs. 8a-b). However,

snout-vent length was related to home range area for male snakes ( $R^2 = 0.735$ ,  $p < 0.002$ ; Fig. 8c):

$$A_l = (1.95 \times 10^{-10}) l^{5.6347}$$

where  $l$  is snake snout-vent length and  $A_l$  is the home range area of a snake of length  $l$ .

## **Habitat selection**

### *Discriminant Function Analysis*

In 2007 and 2008, I measured habitat characteristics (Table 8) at 519 random locations, 123 locations of male timber rattlesnakes in natural areas, 80 locations of males in developed areas, 118 locations of non-gravid females in developed areas, 74 locations of non-gravid females in natural areas, 92 locations of gravid females in developed areas, and 78 locations of gravid females in natural areas.

Box's M test indicated that the assumption of homogeneity of covariance matrices was violated (Box's  $M = 252.97$ ,  $F = 2.89$ ,  $df = 60$ ,  $1417.35$ ,  $p < 0.001$ ). This is a common occurrence with biological data but the basic value of multivariate analyses are routinely defended in spite of these violations as long as the results are ecologically relevant (Reinert 1984a, b; Blouin-Demers and Weatherhead 2001a). The global MANOVA indicated that there were statistically significant differences among group centroids (Wilk's  $\Lambda = 0.009$ ,  $F = 7.77$ ,  $df = 56$ ,  $312.27$ ,  $p < 0.001$ ).

The stepwise model was statistically significant (Wilk's  $\Lambda = 0.019$ ,  $\chi^2 = 257.96$ ,  $df = 28$ ,  $p < 0.001$ ), and included 4 habitat variables (in order of importance) that differentiate habitat use among groups: surface rock, brush, tree density, and relative dominance of eastern redcedar, in order of importance (Table 9, Fig. 9). Gravid female timber rattlesnakes were more likely to use sites with increasing amounts of surface rock,

whereas males and non-gravid females used sites with increasing amounts of brush and higher tree density. Gravid females in natural area used areas with lower cover of eastern redcedar whereas those in the developed area used areas with higher cover. The classification accuracy of the selected DFA model was 61.1%, with most misclassifications among male, female, and random locations.

#### *Logistic Regression Modeling*

Of 46 *a priori* logistic regression models explaining presence of timber rattlesnakes, a model with reproductive status, percent cover of rock, density of trees, and presence of brush piles or coarse woody debris was selected as the best approximating model (Table 4). Presence of gravid female rattlesnakes was positively associated with tree density but negatively associated with percent surface rock and prevalence of brush whereas males and non-gravid females were negatively associated with tree density and positively associated with percent surface rock and prevalence of brush (Table 10). The second-best model was similar to the best model but also included eastern redcedar dominance which had a positive association with gravid female and negative association with male and non-gravid female presence (Table 4, Table 10). Four additional models indicated that rattlesnake habitat use also may have been influenced by average basal area of mast-bearing trees, canopy closure, percent cover of log, and site ( $\Delta AIC_c = 2.73-3.85$ ,  $w_i = 0.09-0.06$ ; Table 4).

## **DISCUSSION**

My finding that gravid female timber rattlesnakes in Wisconsin moved shorter distances and exhibited smaller home ranges than either male or non-gravid female snakes is not surprising given that viviparous snakes often exhibit decreased vagility

during gestation (Shine 1993). Viviparous snakes reduce prey intake during gestation and behaviorally thermoregulate, thereby maximizing embryonic development (Reinert et al. 1984; Reinert and Zappalorti 1988a; Shine 1993; Foster et al. 2009). Thermally suitable habitats with adequate ground cover have been identified as a primary factor in gravid female timber rattlesnake habitat selection (Reinert 1984a, 1984b). These characteristics are exhibited by other species of snakes within the family Viperidae (Vitaanen 1967; Reinert and Kodrich 1982). The relatively large prairie remnants with numerous rock outcrops in my study area likely provided abundant, high quality habitat for gestating female rattlesnakes. Many prairies in state natural areas are actively managed with prescribed fire and several prairies in the residential development burned within the past 10 years as a result of accidental fires. In contrast, the larger home range area of gravid female timber rattlesnakes in the pine barrens of New Jersey (Zappalorti and Mitchell 2008) may be the result of sparse forest openings which require gravid females to move greater distances to find suitable habitat for gestation.

My finding that home range size and movement rate were similar between males and non-gravid females is consistent with home range characteristics for a wide variety of snake species, with home range size typically differing as a result of reproductive status rather than gender (Gregory et al. 1987). In contrast, other studies of timber rattlesnakes showed that males and non-gravid females differed in home range size and movement distance but that home ranges of non-gravid and gravid females were similar (Reinert and Zappalorti 1988a; Sealy 2002; Waldron et al. 2006).

Differences between my results and those of other studies of timber rattlesnakes may be related to sample size and choice of home range estimator. Waldron et al. (2006)

conducted their analyses using 95% fixed kernel estimates of home range, Reinert and Zappalorti (1988a) used 95% isopleth harmonic mean estimates, and I used the MCP estimator. Minimum Convex Polygon home range estimators have been criticized because they may include large areas never used by an animal, whereas kernel and harmonic mean methods estimate home ranges with the recognition that animals do not use all areas of their home range with equal intensity (Dixon and Chapman 1980; Don and Rennolls 1983; White and Garrott 1990). Reinert and Zappalorti (1988a) had a relatively large sample but only included 2 males, 3 non-gravid females, and 2 gravid females in their home range analysis, presumably because they were the snakes in each group that had been tracked for the longest period of time. In contrast, Waldron et al. (2006) pooled gravid and non-gravid females for analysis, although their results largely agree with Reinert and Zappalorti (1988a). Interestingly, my estimates of MCP home ranges for New Jersey rattlesnakes from Reinert and Zappalorti's (1988a) full set of data agree with my MCP results for Wisconsin snakes, namely that male and non-gravid female timber rattlesnakes do not differ in home range area. A notable difference between Wisconsin and New Jersey timber rattlesnakes is a significant difference in home range area for gravid females which I discuss later.

At least some of the differences that I observed in the home range sizes of male, non-gravid, and gravid female timber rattlesnakes can be attributed to differing life history needs of these cohorts. Gravid females seek areas with high insolation and adequate ground cover for enhanced gestation, with regional differences in home range sizes potentially influenced by availability of these habitats. Males consistently exhibit the largest home ranges regardless of estimator or region, probably because they are both



foraging for prey and searching for females, a resource that is widely dispersed. The primary discrepancy between my findings and those of other timber rattlesnake studies involves differences in home range area between non-gravid females and males. Similar to male timber rattlesnakes, non-gravid females are engaged in predatory behavior. However, non-gravid female metabolic requirements may be higher while they regain the several hundred grams they lose during the course of one reproductive event. While non-gravid females may use an area as large as male snakes, their use of that area could be concentrated on several focal points revolving around securing food that may be patchily-distributed but locally abundant (Simon 1975; McLoughlin and Ferguson 2000). When compared to other methods, MCP estimates of home range area may be relatively insensitive to such movements, thereby resulting in the inability to discriminate between males and non-gravid females.

I found a significant correlation between number of days monitored and total distance moved for gravid females but not males or non-gravid females whereas Reinert and Zappalorti (1988a) found a significant correlation for males but not gravid females or non-gravid females.

My findings confirm that timber rattlesnake home range areas and movements vary geographically (Reinert and Zappalorti 1988a; Waldron et al. 2006). Gravid female rattlesnakes from New Jersey had larger total distances moved, average daily distances moved, and MCP home range areas than those from Wisconsin. Furthermore, I found significant differences in home range sizes and movements between gravid females and both males and non-gravid females from Wisconsin, though such differences were not apparent for New Jersey timber rattlesnakes. The relatively large movement distances

and home range sizes exhibited by gravid females in New Jersey may indicate reduced availability of forest openings and other early-successional habitats used by gestating snakes. A potential lack of high-quality habitat for gravid female timber rattlesnakes in New Jersey may be related to the relative rarity of suitable canopy openings in the Pine Barrens region (Zappalorti and Mitchell 2008). In contrast, the Mississippi River bluffs in southwestern Wisconsin are characterized by abundant forest openings. The movement patterns I documented for timber rattlesnakes in Wisconsin, however, are similar to those reported from North Carolina (Sealy 2002, though sample sizes for the latter study were small and the method used to estimate home ranges was not reported).

Regional differences in home ranges and activity patterns of timber rattlesnakes also may be related to prey availability. The frequent forest canopy openings in my study area are maintained by a combination of prescribed fire applied in state natural areas and small clearcuts and other openings associated with residential development along bluffs. Small mammals, the primary prey of timber rattlesnakes, use slash and brush piles associated with natural and human-induced disturbances (Powell and Brooks 1981; Gunther et al. 1983; McComb et al. 1993; Loeb 1999; Converse 2005). Reptiles, including timber rattlesnakes, are commonly associated with forest edges (Zappalorti and Burger 1985; Blouin-Demers and Weatherhead 2001a, b; Kjos and Litvaitis 2001; Zappalorti and Mitchell 2008). Therefore, reduced availability of prey associated with a lack of forest openings in the pine barrens of New Jersey when compared to Wisconsin may at least partially explain differences in timber rattlesnake home range characteristics between the two areas.

Significant differences between home ranges of timber rattlesnakes in Wisconsin and New Jersey were largely driven by differences in movement between gravid females in the two study areas. Additionally, differences in length of tracking period between the two studies may have influenced my comparison because minimum convex polygon home range estimates are particularly sensitive to sample size (Worton 1987; White and Garrott 1990) and several of the smallest home ranges in the New Jersey study were associated with snakes that were tracked for the shortest periods of time (Reinert and Zappalorti 1988a).

I found no significant correlation between number of days tracked and movement of male timber rattlesnakes within my study, but I did find a significant relationship between snout-vent length of male timber rattlesnakes and home range area. Previous research on body size of snakes has largely focused on the relationship between body size and demographic parameters (Blueweiss et al. 1978) and body size-to-home range area relationships, well documented in other taxonomic groups, have been tied to metabolic requirements (i.e., mammals, lizards; see Linstedt et al. 1986; Perry and Garland 2002). In snakes, however, no such relationship has been described. Vitaanen (1967) suggested that distance moved was related to snake length in *Vipera berus*, another of the Viperidae. However, Vitaanen (1967) did not use radio telemetry to monitor movements of the snakes and Gregory et al. (1987) questioned these findings. Although older snakes are generally larger (Heyrend and Call 1951; Clark 1970), age classes overlap greatly in body size, particularly among older snakes, and the validity of using snake length as a surrogate for age is questionable (Parker and Plummer 1987; Macartney et al. 1990). While an age-to-home range area relationship is questionable, my finding of a

length-to-home range area relationship may have conservation implications. Timber rattlesnakes are ambush predators that sit and wait for prey in areas with high probability of encounter (Reinert et al. 1984; Clark 2002, 2007), but such a strategy would be much less effective when focused on a patchy, widely-dispersed resource (i.e., potential mates). The length-home range area relationship in male timber rattlesnakes may be related to mating opportunity, as suggested by McLoughlin and Ferguson (2000).

My analysis of snake movements during five sequential intervals of the active season in southwest Wisconsin revealed only one significant difference in male timber rattlesnake average daily movements. However, this increase in average daily distance moved by male timber rattlesnakes coincided with the beginning of the breeding season for timber rattlesnakes in Wisconsin (mid-July) and similar movements have been noted for male timber rattlesnakes prior to this study (R.A. Sajdak, personal communication). Coupe (2002) identified long, linear movements in male timber rattlesnakes prior to and immediately after periods of contact with a female. Given that larger male snakes are more likely to successfully compete for mates during the ritual combat exhibited by timber rattlesnakes and other vipers (Schuett 1997), large movements made by large snakes within large home ranges should increase their reproductive success. Similarly, large territory size increases mating opportunities in lizards (Salvador et al. 1995; Perry and Garland 2002). Species that breed later in the season when potential mates are widely dispersed from a central location, as in timber rattlesnakes, should have large home ranges which should result in increased breeding opportunity. In contrast, males of species that breed soon after emergence from a central location should increase their opportunity for mating with increased movement early in the season but not necessarily

have large home ranges. For example, male grass snakes (*Natrix natrix*), a species that breeds soon after emerging from the den, made larger movements early in the breeding season and had smaller home ranges than females (Madsen 1984).

I found no length-to-home range area relationship for non-gravid female timber rattlesnakes. Non-gravid female movements may vary depending on prey availability, as has been found in lizards (Simon 1975). Female timber rattlesnakes in this region give birth approximately every third year and can lose up to a third of their body weight from the beginning of a year in which they gave birth to the beginning of the next year (C. Berg, personal communication). Bonnet et al. (2001) identified complex tradeoffs and interactions between use of long-term energy reserves and energy from recently consumed prey on survival and reproductive output in female *Vipera aspis*. A complex relationship between prey availability and home range area may exist for non-gravid female timber rattlesnakes.

Finally, I will touch on the lack of a relationship between snout-vent length and home range area in gravid females. One of the primary habitat selection criteria for gravid female rattlesnakes has been shown to be suitable thermal habitat (Reinert 1984a, 1984b; Foster et al. 2009). Given the thermal ecology associated with viviparity, a lack of relationship between body size and home range size for gravid female timber rattlesnakes is not surprising. Provided there is suitable cover in an area with high insolation, gravid females will be relatively sedentary.

The correlation between number of days tracked and total distance moved for gravid female timber rattlesnakes is partially explained by my analysis of average daily movements across five periods of the active season. Radiotracking for several of the

gravid female snakes had not begun until the end of June. This meant that a large proportion of the gravid snakes were not tracked until after the first part of the active season, which coincided with the most active period for gravid females. The average daily movement of 9.87 m/day during that first time period was greater than during any of the other intervals.

Contrary to my expectations, habitat disturbance did not impact home range area for timber rattlesnakes. I anticipated that habitat impacted by residential development and related changes to natural disturbance regimes would be of lower quality and thereby affect timber rattlesnakes negatively by forcing them to increase home range area to meet their life history needs (Gregory et al. 1987; McLoughlin and Ferguson 2000; Waldron et al. 2006). Home range area of northern watersnakes (*Nerodia sipedon*) did not change as a result of development though movement patterns changed, with snakes in developed areas showing higher site fidelity to certain areas within their home range, presumably because the amount of high-quality habitat within their home ranges had been reduced (Pattishall and Cundall 2008). Development in the impacted study site from my study occurred at a relatively low density (<0.1 house/ha) with nearly all development on land that had previously been in agricultural use for hay, corn, or soybeans. Otherwise, changes from a timber rattlesnake's perspective may have been minimal because most open fields were still mowed several times per year for hay or to control noxious weeds and residential development resulted in only minor changes to forested portions of the site. Most land around the site is on steep terrain, which led to retention of relatively contiguous strips of forest interrupted by occasional narrow clearcuts to enhance landowners' views of the Upper Mississippi River. Landscape connectivity is generally

maintained when greater than 60% of available cover is suitable habitat, even for an area-sensitive species (Andren 1994; Turner et al. 2001). That number may be lower for a geographically widespread species like the timber rattlesnake, which appears to be a habitat generalist (Steen et al. 2007). Habitat loss is the primary impact on species until suitable habitat drops below 30% of available habitat, at which point landscape connectivity is impacted due to small patch size and isolation of patches (Andren 1994). In addition, some snake species use human-disturbed habitats in developed areas and habitat edge in urbanized areas can serve as a substitute for early-successional habitat that occurred under natural disturbance regimes (Kjoss and Litvaitis 2001; Zappalorti and Burger 1985; Zappalorti and Mitchell 2008).

I found that timber rattlesnake home ranges substantially overlapped indicating that the timber rattlesnakes do not defend large areas and are probably not territorial. In fact, timber rattlesnakes have been found to be attracted to areas occupied by their congeners (Clark 2007).

I found gravid snakes selected open, sunny areas with abundant rock cover, while males and non-gravid females selected more heavily-forested areas, which agrees with previous findings on timber rattlesnake habitat selection (Reinert 1984a, b; 1993). The different methods of analysis resulted in models containing the same variables but with slightly different interpretations. This is because habitat selection can differ based on the spatial scale of observation (Wiens et al. 1987; Wiens 1989). The logistic regression models also indicate that gravid female timber rattlesnakes selected specific locations with slightly less surface rock and higher tree density than typically available within their home range. This may be because woody species in the prairies tend to be relatively

more abundant on and near rock outcrops, where they were protected during previous fires. The logistic models also indicated that males and non-gravid females selected specific locations with slightly lower density of trees than was typically available within their home range. They often selected small openings within forested areas, probably for basking.

I included the variable assessing the importance of the presence of brush piles because of their prevalence in the developed area within my study. While maintaining coarse woody debris as a habitat feature is touted as important for herpetofauna (Douglass and Reinert 1982; Bailey et al. 2006; Mitchell et al. 2006), I have found no research quantifying slash or brush piles habitat use by snakes. While downed trees provided similar cover in forested areas, the brush and slash piles in the developed area resulted from property maintenance and land-clearing activities and were often associated with the small clearcuts that nearly all landowners made to enhance their view of the Mississippi River, with other piles from tree trimming and brush removal sometimes scattered around properties. The habitat selection analyses confirmed my observations that timber rattlesnakes were making considerable use of brush piles within the developed site, often using them to “island hop” across open areas. These brush piles were placed in areas more open than what is typically cited as habitat for male and non-gravid female timber rattlesnakes. However, timber rattlesnakes that use brush piles may benefit. Beyond the obvious cover they provide, brush piles may harbor significant numbers of prey based on studies of small mammal association with the slash found in clearcut and managed forests (Powell and Brooks 1981; Gunther et al. 1983; McComb et al. 1993; Loeb 1999; Converse 2005). In addition, timber rattlesnakes may receive additional



benefits relating to either ecdysis or digestion of captured prey (Peterson et al. 1993; Blouin-Demers and Weatherhead 2001b).

I included a variable measuring the relative predominance of eastern redcedar because it can be invasive in areas where habitat disturbance from fire has been eliminated and, as a consequence, is a focus of management activities aimed at restoring native prairie and associated oak woodland on bluffs overlooking the Mississippi River and many of its tributaries in Wisconsin, Minnesota, and Iowa. Eastern redcedar is common throughout the region and is often associated with rock outcrops within bluff prairie habitats. Once established, eastern redcedar can completely shade a rock outcrop. This is potentially problematic because gravid female timber rattlesnakes rely on open, sunny areas with an abundance of rocky cover to elevate their body temperature, which enhances embryonic development (Reinert et al. 1984; Reinert and Zappalorti 1988a; Shine 1993; Foster et al. 2009). Therefore, excessive shading of rocky habitats by eastern redcedar could indirectly affect reproductive output of timber rattlesnakes by reducing opportunities to effectively regulate body temperature during gestation in close proximity to cover.

Like the home range area analyses, I expected to find a difference in habitat selection between the natural area and the developed site. The axes of the discriminant function analyses only provided a clear separation between the developed and natural sites with the third discriminant function, which identified a separation between gravid females from different sites. Gravid females had already been separated from males, non-gravid females, and random locations based on the first function with gravid females using relatively more rocky habitats. Gravid females from both natural and developed

sites selected rocky habitats but gravid snakes in the natural sites selected locations with low relative dominance of eastern redcedar and gravid females in developed sites selected locations with high relative dominance of eastern redcedar. My interpretation is that, given a choice, gravid female timber rattlesnakes will select habitats with relatively less eastern redcedar which supports the notion that increases in the amount of eastern redcedar on bluff habitats could negatively affect gravid female timber rattlesnakes. However, neither of the logistic regression models receiving substantial support identified site effects as important for timber rattlesnakes. A model receiving limited support, however, did identify site as a variable but there was little evidence in its favor.

The overall results of my study would seem to indicate that the timber rattlesnake is capable of persisting at this level of development, possibly because the effects of habitat fragmentation are not excessive (Andren 1994). Other large snake species have been documented to persist in rural areas with some development, seemingly because they are capable of utilizing artificial habitats and their ecology does not require constant movement (Shine and Fitzgerald 1996). Based on the results of my home range and habitat selection analyses, this may be the case for the timber rattlesnake, which has been described as a habitat generalist (Steen et al. 2007). While this may indeed be the case, the timber rattlesnake is a long-lived species with relatively low reproductive output. Small reductions in survival rates could have relatively large impacts. Only 1 of the 6 largest male timber rattlesnakes I captured during the two years of this study was found in the developed area in spite of intensive search efforts, which is noteworthy. While this is only anecdotal evidence, low numbers of large male timber rattlesnakes could indicate lower survival in the large males found near developments because of their increased

exposure to humans and roads within their home ranges (Rudolph and Burgdorf 1997; Andrews and Gibbons 2008). This sort of effect could have subsequent impacts on connectivity among populations (Driscoll 2004; Blouin-Demers and Weatherhead 2002).

An evident limitation of this study is the lack of replication for developed and natural areas, which limits the certainty of the results. The 34 timber rattlesnakes whose movements I monitored are pseudoreplicates of site treatments, making the major limitation of this study the lack of replication for developed and natural areas (Hurlbert 1984). This limits any conclusions of similarities or differences to the comparison of these two sites.

The six dens are relatively near one another and within the same developed and natural areas, which raises questions about their statistical independence. Statistical independence among timber rattlesnakes, in particular, may be problematic. Young timber rattlesnakes have been documented following adults on their way to hibernacula (Reinert and Zappalorti 1988b). Even beyond their juvenile stage movements, habitat selection, and foraging patterns of timber rattlesnakes may be influenced by congeners (Clark 2007). The potential effects of conspecific scent trailing are nearly impossible to assess, certainly for this study. No real difference in home range area of timber rattlesnakes may, in fact, occur at the intensity of development found in my study area. Unfortunately, budget limitations and logistical considerations prevented us from conducting the study at multiple sites for each of the disturbance treatments.

## **MANAGEMENT IMPLICATIONS**

Characterizing patterns of movement and habitat use is critical for understanding the basic ecology and behavior of a species (Gregory et al. 1987; Reinert and Zappalorti

1988a; Roe et al. 2004). Furthermore, description of home range size and other habitat parameters can provide guidelines for conservation and management, including programs that set aside areas of critical habitat for the purpose of conserving viable populations (Roe et al. 2004). My research is the first effort to quantify home range size and habitat use of timber rattlesnakes in Wisconsin and is an important step for conservation of the species in this region.

My finding that gravid females have significantly smaller home range areas than either non-gravid female or male timber rattlesnakes makes clear that they are not area-sensitive. Combined with the results of my habitat selection analyses, retention of key habitat features is clearly a high priority when managing for gravid female timber rattlesnakes. Specifically, habitat restoration efforts that are intended to benefit timber rattlesnakes should focus on enhancement of habitat at known den locations by providing gravid females with adequate access to rocky outcrops in areas with low canopy cover. My results further indicate that eastern redcedar should be targeted for removal. In addition, research identifying the potential costs to reproductive output of gravid female timber rattlesnakes in areas with encroaching eastern redcedar could provide important insights into the importance of habitat restoration efforts that remove eastern redcedar.

On the other hand, male timber rattlesnakes appear to be area-sensitive. Management for male timber rattlesnakes will be complicated by continuing development of Mississippi River bluffs. Snake mortality on roads is a conservation problem, particularly because some roadkill is intentional (Ashley et al. 2007). A wide-ranging animal like the male timber rattlesnake will suffer higher mortality with increasing development, particularly as a result of road mortality but also because of increased

exposure to humans (Rudolph and Burgdorf 1997; Bonnet et al. 1999; Andrews and Gibbons 2008). Of particular concern in this regard is my finding that home range area increased with snake size. The most wide-ranging, and presumably most dominant, males will be at greatest risk from development (Bonnet et al. 1999). Management actions to benefit males should include mitigative measures associated with road building. My habitat analysis indicated that timber rattlesnake movements within developed areas may be guided by enhancing specific areas with brush piles and maintaining corridors for connectivity. Such actions could be combined with road-building mitigation to significantly reduce timber rattlesnake mortality. Monitoring should be incorporated into any conservation designs because maintaining corridors may be insufficient for successful conservation (Harrison and Bruna 1999).

To address direct mortality from landowners, education efforts should be increased. Conservation agencies and non-profit conservation organizations should work with individual landowners to promote timber rattlesnake conservation because one of the major challenges facing snakes in general and venomous species like the timber rattlesnake in particular is killing by humans (Brown 1993; Dodd 1993). Again, my findings regarding timber rattlesnake use of brush piles provides a simple tool to reduce human-rattlesnake conflicts. By encouraging landowners to strategically place brush piles in areas with minimal human activity, the potential for a venomous snake bite could be reduced while maintaining habitat connectivity for timber rattlesnakes in developed areas. Timber rattlesnakes appear to have flexibility in their home range habitat requirements that could allow them to persist in the presence of humans, but only if direct mortality on adult snakes can be minimized. The challenges lie in taking a proactive

approach by addressing development practices and human dimensions of snake conservation before further development complicates the undertaking.

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**Table 1.** Habitat variables measured at used and random locations within timber rattlesnake (*Crotalus horridus*) home ranges, southwestern Wisconsin.

Variable abbreviation	Units	Description
CAN	%	Average % canopy closure measured at snake location
DOST	m	Distance to nearest overstory tree (DBH $\geq 7.5$ cm, height $\geq 2$ m) in each quadrant
DBH	cm	Diameter at breast height of nearest overstory tree in each quadrant
TRSP	-	Species of nearest overstory tree in each quadrant
DUNT	m	Distance to nearest understory tree (DBH $\leq 7.5$ cm, height $\geq 2$ m) in each quadrant
DLOG	m	Distance to nearest woody debris (diameter $\geq 7.5$ cm)
LOGDI	cm	Diameter of nearest log
ROCK	%	% rock cover within 1-m <sup>2</sup> centered on snake
LROCK	cm	Length of largest rock $\geq 10$ cm that encroaches into 1-m <sup>2</sup> centered on snake
LEAF	%	% leaf litter cover within 1-m <sup>2</sup> centered on snake
HVEG	%	% herbaceous cover within 1-m <sup>2</sup> centered on snake
JNPR	%	% of 1-m <sup>2</sup> centered on snake with eastern redcedar directly above
LOG	%	% cover of woody debris (diameter $\geq 7.5$ cm) within 1-m <sup>2</sup> centered on snake

WSNUM	#	Number of woody stems present within 1-m <sup>2</sup> centered on snake
WSHT	cm	Height of tallest woody stem ≤2 m tall within 1-m <sup>2</sup> centered on snake
HERB	Y/N	Herbaceous vegetation present in single block ≥20% of 1-m <sup>2</sup> centered on snake
VINE	Y/N	Creeping vegetation present in single block ≥20% of 1-m <sup>2</sup> centered on snake
SHRUB	Y/N	Woody stem cover present in single block ≥20% of 1-m <sup>2</sup> centered on snake
GRJU	Y/N	<i>J. communis</i> present in single block ≥20% of 1-m <sup>2</sup> centered on snake
BRUSH	Y/N	Brushy debris present in single block ≥20% of 1-m <sup>2</sup> centered on snake

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**Table 2.** Variables analyzed during discriminant function analysis of timber rattlesnake (*Crotalus horridus*) habitat selection parameters.

Variable abbreviation	Units	Description
CAN	%	Percent canopy closure
MAST	m <sup>2</sup> /ha	Average basal area of combined mast-bearing species ( <i>Quercus</i> sp., <i>Carya</i> sp., <i>Juglans nigra</i> )
JNPRRD	%	Basal dominance of eastern redcedar relative to all species
ROCK	%	% rock cover within 1-m <sup>2</sup> centered on snake
TDENS	stems/ha	Density of overstory trees
LOG	%	% cover of woody debris (diameter $\geq 7.5$ cm) within 1-m <sup>2</sup> centered on snake
BRUSH	#	Proportion of locations with brushy debris occurring as a single block $\geq 20\%$ of 1-m <sup>2</sup> centered on snake



**Table 3.** Variables used in logistic regression analyses of timber rattlesnake (*Crotalus horridus*) habitat selection parameters.

Variable abbreviation	Units	Description
MAST	m <sup>2</sup> /ha	Average basal area of combined mast-bearing species ( <i>Quercus</i> sp., <i>Carya</i> sp., <i>Juglans nigra</i> )
JNPRRD	%	Basal dominance of eastern redcedar relative to all species
ROCK	%	% rock cover within 1-m <sup>2</sup> centered on snake
TDENS	stems/ha	Density of overstory trees
CAN	%	Percent canopy closure
LOG	%	% cover of woody debris (diameter $\geq 7.5$ cm) within 1-m <sup>2</sup> centered on snake
BRUSH	#	Proportion of locations with brushy debris occurring as a single block $\geq 20\%$ of 1-m <sup>2</sup> centered on snake
NONGRAVID	Y/N	Snake is either a male or a non-gravid female, the reference category for logistic regression analyses.
SITE	Y/N	Natural area

**Table 4.** Logistic regression models explaining the influence of different habitat characteristics and snake attributes on habitat selection of timber rattlesnakes (*Crotalus horridus*) with associated model ranks (based on Akaike’s Information Criterion corrected for small sample size [AIC<sub>c</sub>]).

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	ΔAIC <sub>c</sub> <sup>d</sup>	w <sub>i</sub> <sup>e</sup>
NONGRAVID, ROCK, TDENS, BRUSH	5	33.76	0.00	0.41
NONGRAVID, ROCK, TDENS, BRUSH, JNPRRD	6	34.87	1.11	0.24
NONGRAVID, ROCK, TDENS, BRUSH, SITE	6	36.49	2.73	0.11
NONGRAVID, ROCK, TDENS, BRUSH, JNPRRD, MAST	7	36.87	3.11	0.09
NONGRAVID, ROCK, TDENS, BRUSH, JNPRRD, MAST, CAN, LOG	9	37.61	3.84	0.06
NONGRAVID, ROCK, TDENS, BRUSH, JNPRRD, SITE	7	37.62	3.85	0.06
NONGRAVID, ROCK, TDENS, BRUSH, JNPRRD, MAST, SITE	8	39.65	5.89	0.02
NONGRAVID, ROCK, TDENS, BRUSH, JNPRRD, MAST, CAN, LOG, SITE	10	41.41	7.64	0.01
NONGRAVID, ROCK, BRUSH, CAN	5	44.87	11.10	0.00
NONGRAVID, ROCK, BRUSH, CAN, SITE	6	45.85	12.09	0.00
NONGRAVID, ROCK, BRUSH, JNPRRD, MAST, CAN	7	47.30	13.54	0.00
NONGRAVID, ROCK, BRUSH, JNPRRD, MAST, CAN, LOG, SITE	8	47.70	13.94	0.00

CAN, SITE				
NONGRAVID, ROCK, TDENS, SITE	5	48.47	14.70	0.00
NONGRAVID, ROCK, TDENS	4	48.92	15.16	0.00
NONGRAVID, ROCK, JNPRRD, TDENS	5	50.24	16.47	0.00
NONGRAVID, ROCK, BRUSH	4	50.94	17.18	0.00
NONGRAVID, ROCK, TDENS, JNPRRD, SITE	6	51.19	17.42	0.00
NONGRAVID, BRUSH	3	52.24	18.47	0.00
NONGRAVID, ROCK, BRUSH, SITE	5	52.46	18.70	0.00
NONGRAVID, ROCK, CAN, LOG	5	53.27	19.50	0.00
NONGRAVID, ROCK, BRUSH, JNPRRD, SITE	6	54.65	20.89	0.00
NONGRAVID, ROCK, BRUSH, JNPRRD	5	55.04	21.27	0.00
NONGRAVID, ROCK, CAN, LOG, SITE	6	56.03	22.26	0.00
NONGRAVID, BRUSH, SITE	4	58.93	25.17	0.00
NONGRAVID, BRUSH, TDENS, SITE	5	59.32	25.55	0.00
NONGRAVID, BRUSH, TDENS	4	60.20	26.43	0.00
NONGRAVID, ROCK, CAN	4	61.69	27.93	0.00
NONGRAVID, ROCK	3	63.36	29.60	0.00
NONGRAVID, ROCK, CAN, SITE	5	64.40	30.63	0.00
NONGRAVID, ROCK, SITE	4	67.68	33.92	0.00
NONGRAVID, ROCK, JNPRRD	4	70.91	37.15	0.00
NONGRAVID, JNPRRD	3	72.82	39.06	0.00
NONGRAVID, ROCK, JNPRRD, SITE	5	73.20	39.44	0.00
NONGRAVID, BRUSH, JNPRRD, SITE	5	75.77	42.00	0.00

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NONGRAVID, BRUSH, JNPRRD	4	76.71	42.94	0.00
NONGRAVID, TDENS, JNPRRD, SITE	5	79.34	45.58	0.00
NONGRAVID, TDENS, SITE	4	79.34	45.58	0.00
NONGRAVID, TDENS, JNPRRD	4	79.58	45.82	0.00
NONGRAVID, JNPRRD, SITE	4	80.71	46.95	0.00
NONGRAVID, TDENS	3	85.05	51.29	0.00
NONGRAVID, MAST	3	92.49	58.73	0.00
NONGRAVID, JNPRRD, CAN	4	94.80	61.04	0.00
NONGRAVID, MAST, SITE	4	95.01	61.25	0.00
NONGRAVID, JNPRRD, CAN, SITE	5	97.38	63.61	0.00
NONGRAVID, CAN	3	97.80	64.04	0.00
NONGRAVID, CAN, SITE	4	98.46	64.70	0.00

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<sup>a</sup> Model parameters from Table 6, number includes intercept.

<sup>b</sup> Number of estimable parameters in approximating model.

<sup>c</sup> Akaike's Information Criterion corrected for small sample size.

<sup>d</sup> Difference in value between  $AIC_c$  of the current model versus the best approximating model ( $AIC_{cmin}$ ).

<sup>e</sup> Akaike weight. Probability that the current model (*i*) is the best-approximating model among the set of candidate models.

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**Table 5.** Tracking information and activity parameters for timber rattlesnakes (*Crotalus horridus*) in southwest Wisconsin (M = male, G = gravid female, F = non-gravid female; subscripts: d = developed site, n = state natural area).

Snake number	Sex	Total length (cm)	Number of days tracked	Number of locations	Total distance moved (m)	Dist./day (m)	Home range area (ha)
159	F <sub>d</sub>	96.5	104	19	2924.1	28.12	35.03
187	F <sub>d</sub>	85.0	93	17	1035.1	11.13	1.93
299	F <sub>d</sub>	88.2	111	19	4232.3	38.13	42.91
362f	F <sub>d</sub>	103.0	75	14	2461.4	32.82	19.59
610f	F <sub>d</sub>	92.0	92	21	1442.5	15.68	11.33
760	F <sub>d</sub>	98.0	85	16	5116.7	59.50	57.43
862	F <sub>d</sub>	93.0	111	20	2238.9	20.17	13.41
422	F <sub>n</sub>	105.5	81	16	1852.0	22.86	15.53
878f	F <sub>n</sub>	91.0	81	19	1283.8	15.85	4.47
889	F <sub>n</sub>	94.0	97	21	1652.2	17.03	4.60
901	F <sub>n</sub>	102.5	133	19	2515.2	189.91	31.92
110g	G <sub>d</sub>	94.5	119	22	405.0	3.40	0.47
362g	G <sub>d</sub>	105.5	108	19	328.3	3.04	0.42
494	G <sub>d</sub>	94.5	78	15	236.1	3.03	0.15
610g	G <sub>d</sub>	90.0	78	14	572.0	7.33	0.70
950	G <sub>d</sub>	93.5	123	21	666.7	5.42	1.43
240	G <sub>n</sub>	106.0	138	21	992.2	7.19	3.46

461	G <sub>n</sub>	97.5	80	14	415.3	5.19	0.63
705	G <sub>n</sub>	104.0	101	19	470.4	4.66	0.34
746	G <sub>n</sub>	90.0	82	14	452.6	5.52	1.38
878g	G <sub>n</sub>	92.0	101	18	653.1	6.47	0.67
089	M <sub>d</sub>	75.2	104	15	766.0	7.37	1.71
110d	M <sub>d</sub>	98.5	123	21	3350.5	27.24	25.02
380	M <sub>d</sub>	111.0	108	21	2994.5	27.73	28.25
398	M <sub>d</sub>	113.0	88	17	5216.2	59.28	64.50
802	M <sub>d</sub>	82.0	106	18	2463.4	23.24	13.50
040	M <sub>n</sub>	93.5	90	17	2243.6	24.93	7.19
279	M <sub>n</sub>	97.0	111	19	3164.0	28.50	19.94
339	M <sub>n</sub>	121.0	113	21	4125.0	36.50	46.23
727	M <sub>n</sub>	129.0	115	20	6133.9	53.34	82.30
821	M <sub>n</sub>	98.5	90	16	2688.6	29.87	15.58
919	M <sub>n</sub>	93.5	131	17	4089.6	31.22	46.65
940	M <sub>n</sub>	77.0	131	21	1992.9	15.21	8.40
961	M <sub>n</sub>	122.5	109	22	6346.9	58.23	107.50

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**Table 6.** Means and standard errors (in parentheses) of activity parameters for timber rattlesnake (*Crotalus horridus*) group by site.

Site	Group	Total distance moved (m)	Average distance/day (m)	Home range area (ha)
Developed ( <i>n</i> = 17)	Non-gravid female ( <i>n</i> = 7)	2778.71 *	29.36 †	25.95 ‡
	Gravid female ( <i>n</i> = 5)	441.61 **	4.44 ††	0.63 ‡‡
	Male ( <i>n</i> = 5)	2958.13 *	28.97 †	26.60 ‡
Natural ( <i>n</i> = 17)	Non-gravid female ( <i>n</i> = 4)	1825.78 *	18.66 †	14.13 ‡
	Gravid female ( <i>n</i> = 5)	596.70 **	5.80 ††	1.30 ‡‡
	Male ( <i>n</i> = 8)	3848.07 *	34.73 †	41.60 ‡

\*, \*\*, †, etc. Shared superscripts indicate homogeneous subgroups based on Tukey's HSD ( $p = 0.05$ ).

**Table 7.** Proportion of minimum convex polygon home range overlap between timber rattlesnakes (*Crotalus horridus*). (Read table as: “Proportion of snake [row] MCP home range shared with snake [column].”)

Snake Number	279	339	727	901	919	940
279	1	0.51	0.88	0.03	0.50	0.09
339	0.22	1	0.90	0.52	0.25	0.00
727	0.21	0.51	1	0.25	0.37	0.00
901	0.02	0.75	0.63	1	0.10	0.00
919	0.22	0.26	0.66	0.07	1	0.00
940	0.21	0.01	0.02	0.00	0.00	1



**Table 8.** Group means and standard errors (in parentheses) for habitat variables used in habitat selection model development.

Variable	Developed Site				Natural Site			
	Random <i>n</i> = 18	Male <i>n</i> = 5	Non- gravid Female <i>n</i> = 8	Gravid Female <i>n</i> = 5	Random <i>n</i> = 18	Male <i>n</i> = 8	Non- gravid Female <i>n</i> = 5	Gravid Female <i>n</i> = 5
CAN	79.0 (3.65)	68.9 (3.62)	72.7 (5.15)	51.7 (4.57)	63.1 (1.47)	63.0 (2.92)	61.5 (7.60)	26.4 (6.64)
AVGBA	20.7 (2.20)	6.8 (1.11)	11.9 (2.67)	4.1 (1.81)	15.4 (0.59)	18.6 (2.71)	15.5 (4.23)	0.9 (0.32)
MAST	12.4 (2.12)	3.8 (0.95)	7.1 (1.95)	1.5 (1.15)	10.0 (0.42)	11.0 (1.79)	7.5 (3.17)	0.5 (0.17)
JNPRRD	12.7 (3.84)	7.7 (1.47)	8.4 (1.92)	49.2 (13.46)	1.6 (0.19)	0.6 (0.39)	0.0 (0.00)	0.6 (0.35)
ROCK	7.8 (2.06)	4.3 (1.44)	6.7 (2.14)	53.0 (3.70)	4.2 (0.29)	14.4 (5.58)	2.7 (1.42)	63.1 (2.93)
TDENS	597.2 (53.51)	239.8 (36.79)	338.6 (66.18)	205.6 (75.76)	292.0 (10.55)	249.0 (22.69)	221.1 (68.27)	35.9 (9.15)
LOG	1.06 (0.19)	7.5 (2.27)	4.3 (1.27)	1.5 (1.37)	1.8 (0.10)	4.4 (0.87)	3.8 (1.40)	0.5 (0.50)
BRUSH	5.4 (1.78)	35.5 (6.31)	32.0 (4.38)	7.3 (5.21)	5.6 (0.38)	11.8 (2.35)	23.8 (8.14)	3.7 (1.52)

**Table 9.** Standardized canonical discriminant function coefficients for the four significant functions describing timber rattlesnake (*Crotalus horridus*) habitat use in southwest Wisconsin.

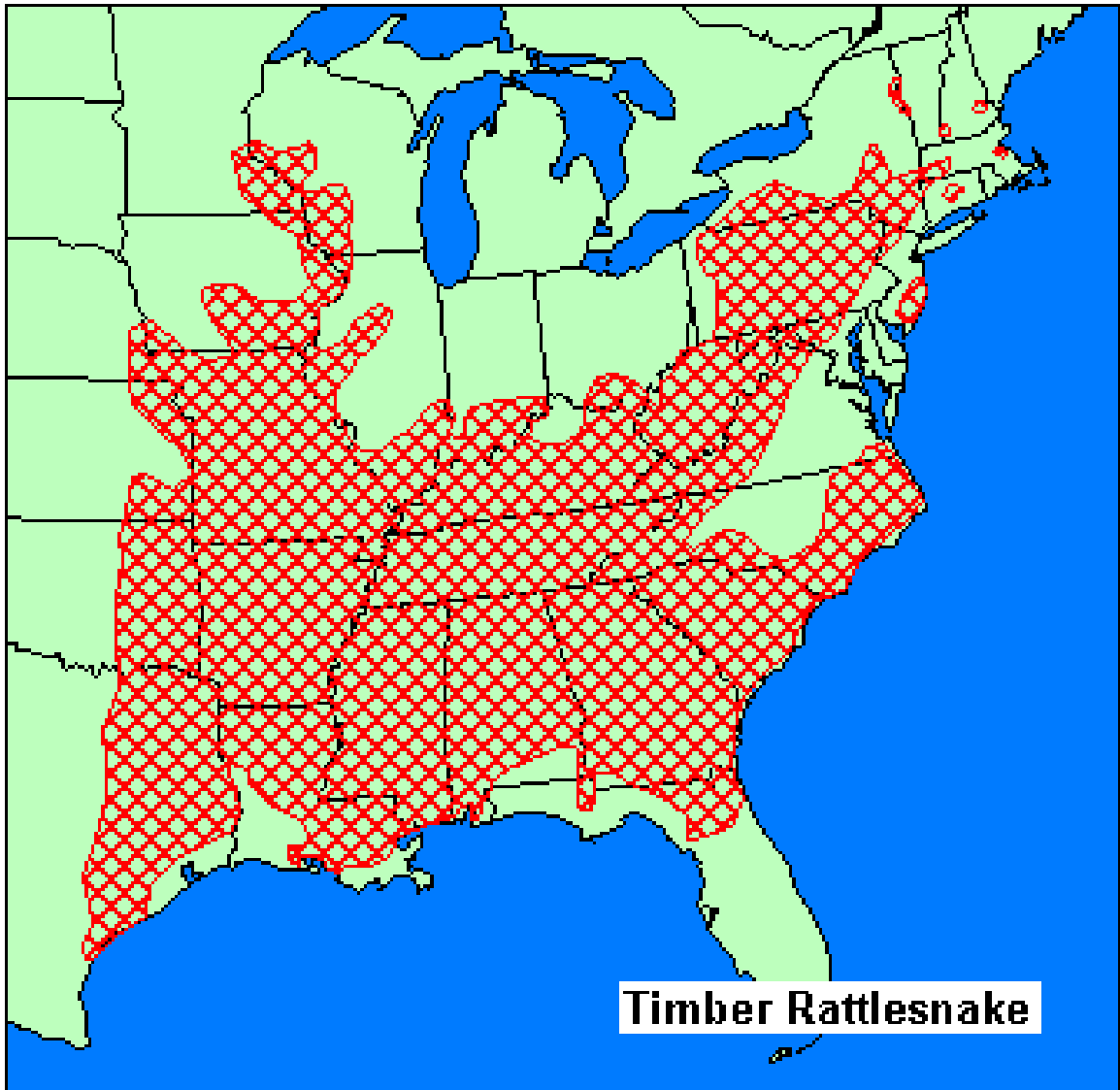
Variable	Function			
Rock	0.996	0.010	-0.065	0.314
Tree density	0.004	-0.576	0.417	0.748
Brush	-0.051	0.923	0.293	0.350
Juniper relative dominance	-0.008	0.075	0.925	-0.466

**Table 10.** Parameter estimates ( $\beta$ ) and standard errors (SE) from the best approximating models explaining the influence of snake and habitat attributes on habitat selection in timber rattlesnakes (*Crotalus horridus*). <sup>a</sup>

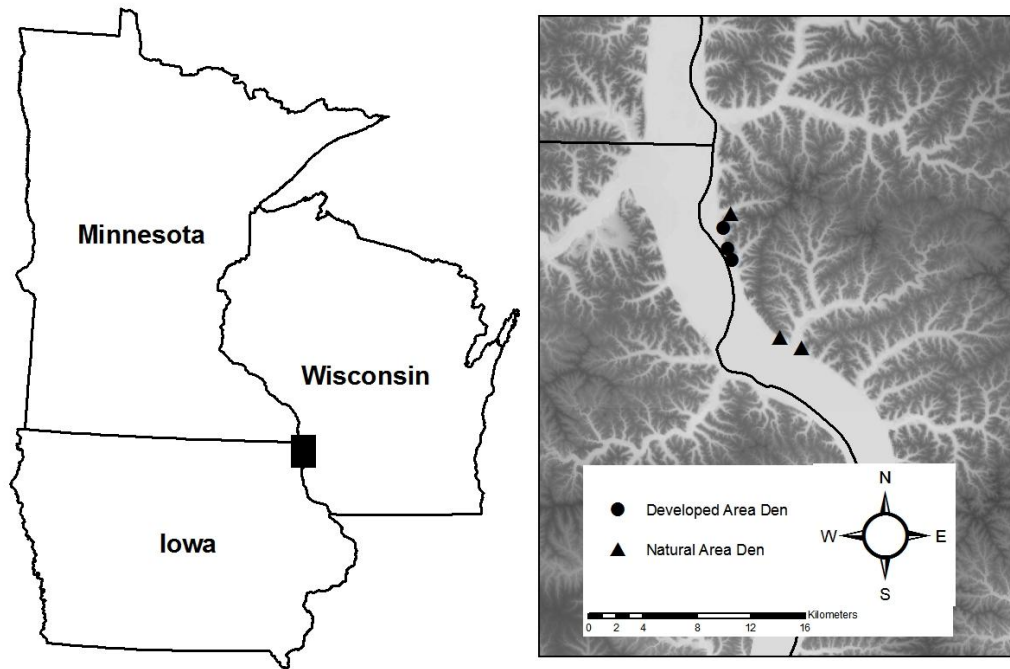
Model	$\beta$	SE	$R^2$ <sup>b</sup>
Best Approximating Model			
Constant	-1.692	1.574	0.882
NONGRAVID	13.959	7.903	
ROCK	-0.436	0.192	
TDENS	0.018	0.008	
BRUSH	-22.694	9.057	
Second-best Approximating Model			
Constant	-1.874	1.565	0.893
NONGRAVID	22.930	13.413	
ROCK	-0.473	0.223	
TDENS	0.022	0.009	
BRUSH	-25.253	10.204	
JNPRRD	-15.529	12.567	

<sup>a</sup> Male and non-gravid female snakes are the reference category for sex/reproductive status (NONGRAVID).

<sup>b</sup> Nagelkerke's rescaled  $R^2$



**Fig. 1.** Range of the timber rattlesnake (*Crotalus horridus*) in the United States (from New York State Department of Environmental Conservation Timber Rattlesnake Fact Sheet accessed on March 29, 2008 at <http://www.dec.ny.gov/animals/7147.html>).

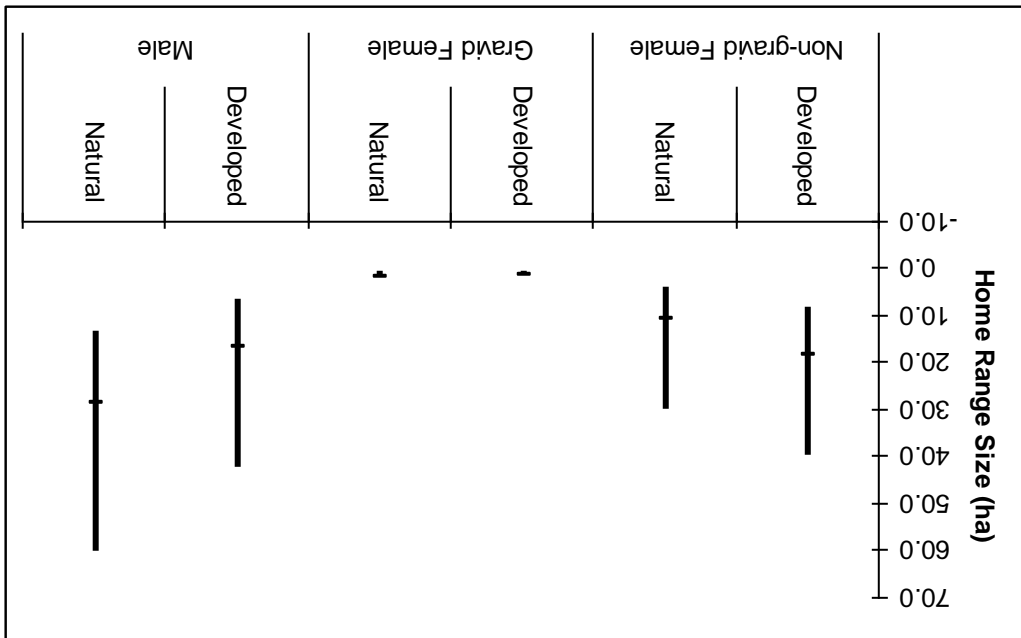


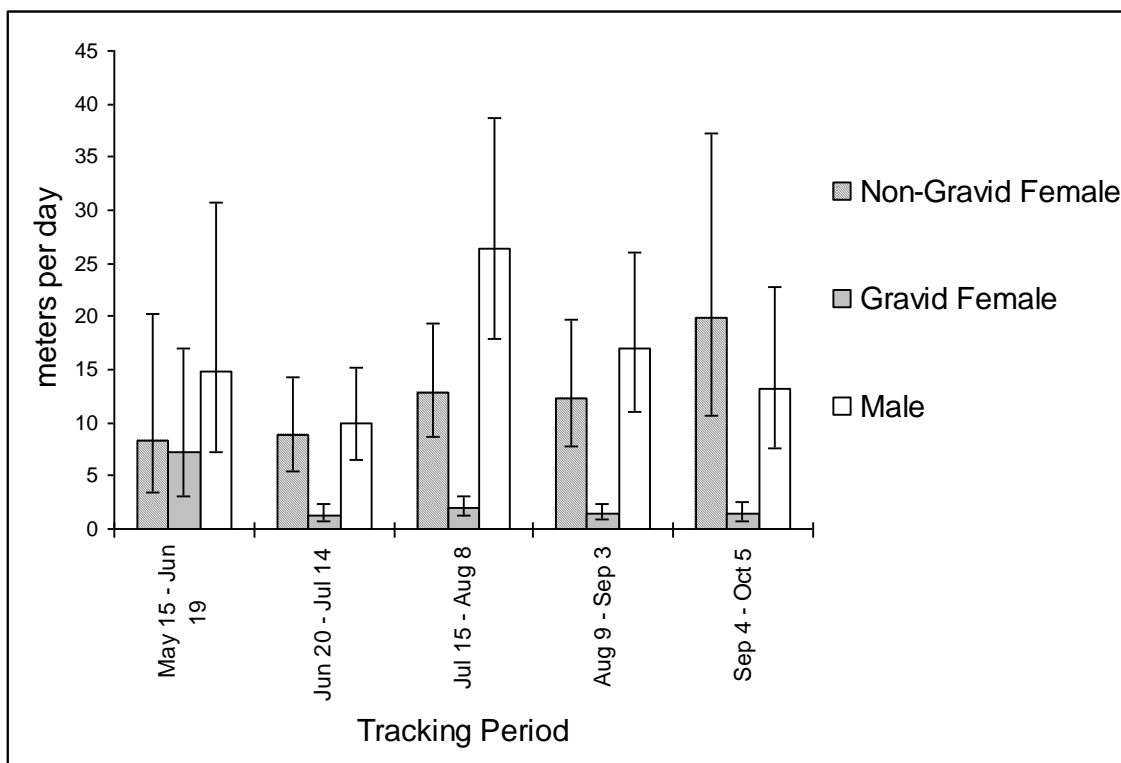
**Fig. 2.** Map of study area in southwestern Wisconsin and locations of timber rattlesnake (*Crotalus horridus*) dens in developed and natural areas.



**Fig. 3.** Typical home ranges for male (#380), non-gravid female (#159), and gravid female (#110) timber rattlesnakes (*Crotalus horridus*) in southwestern Wisconsin, 2007-2008.

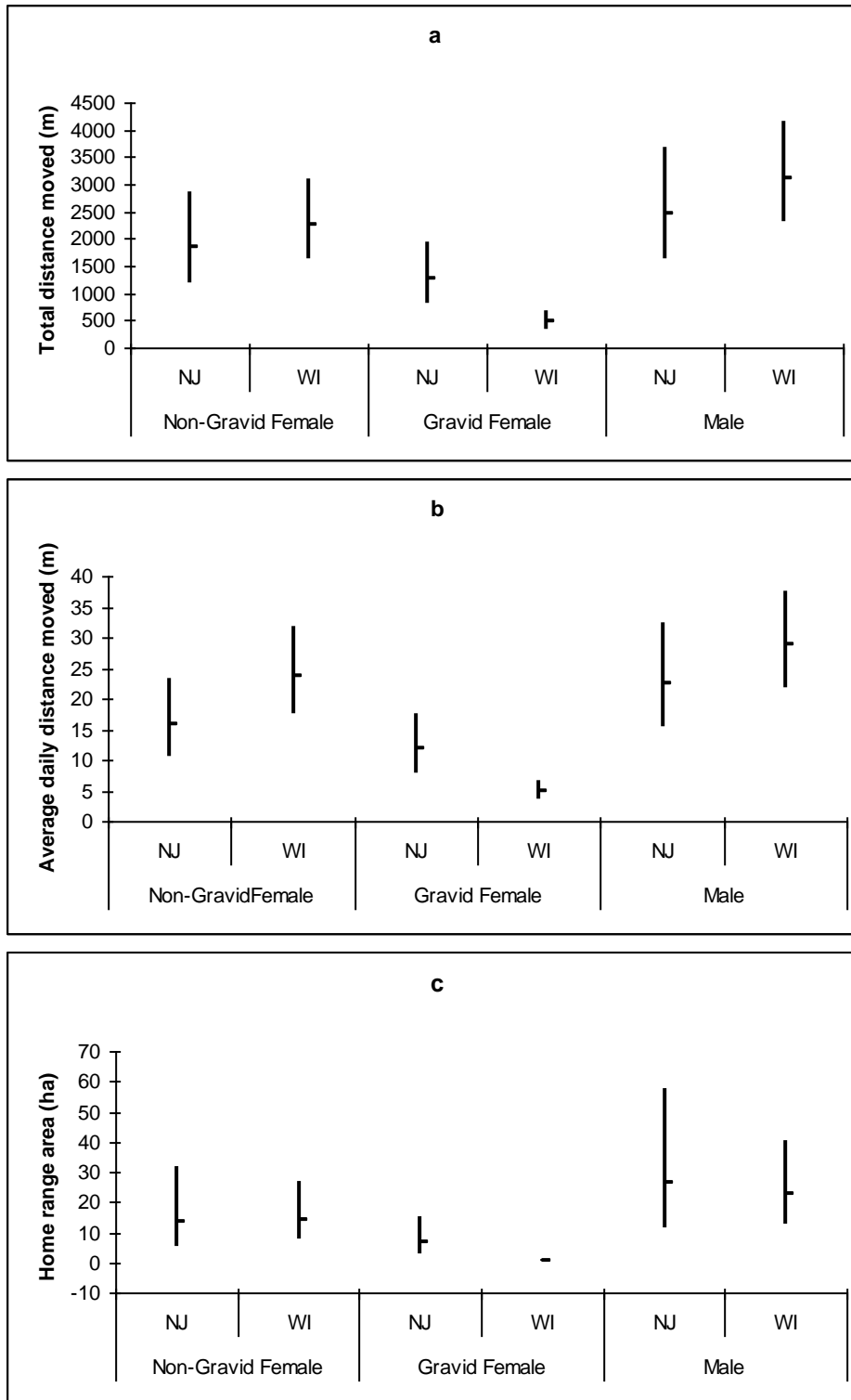
**Fig. 4.** Backtransformed log average home range area and 95% confidence interval for timber rattlesnakes (*Crotalus horridus*) in southwest Wisconsin by group and site.



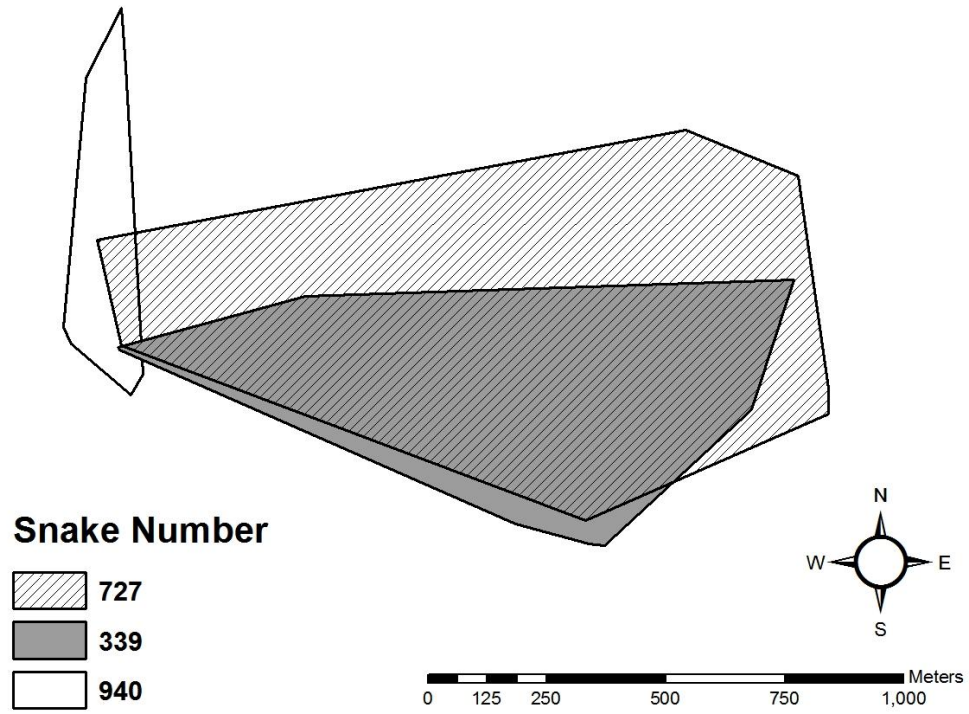


**Fig. 5.** Average daily distance moved and 95% confidence intervals for timber rattlesnakes (*Crotalus horridus*) during 5 intervals of the 2007 and 2008 active seasons in southwestern Wisconsin.

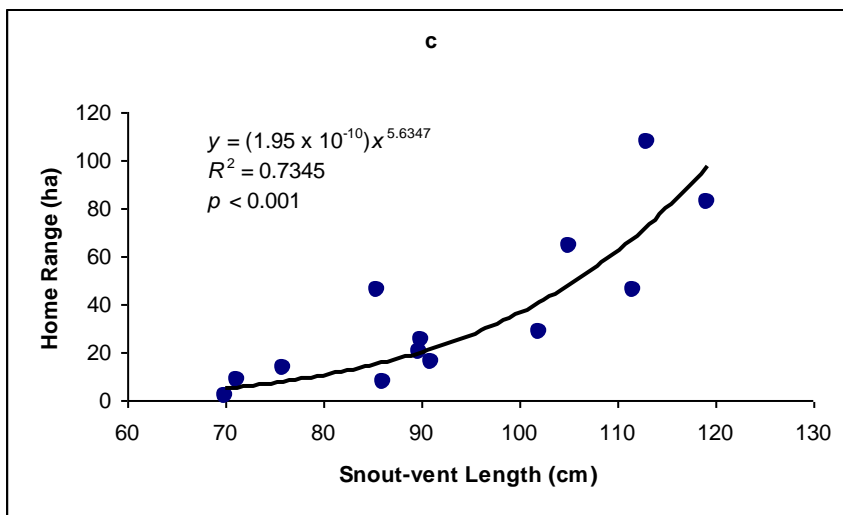
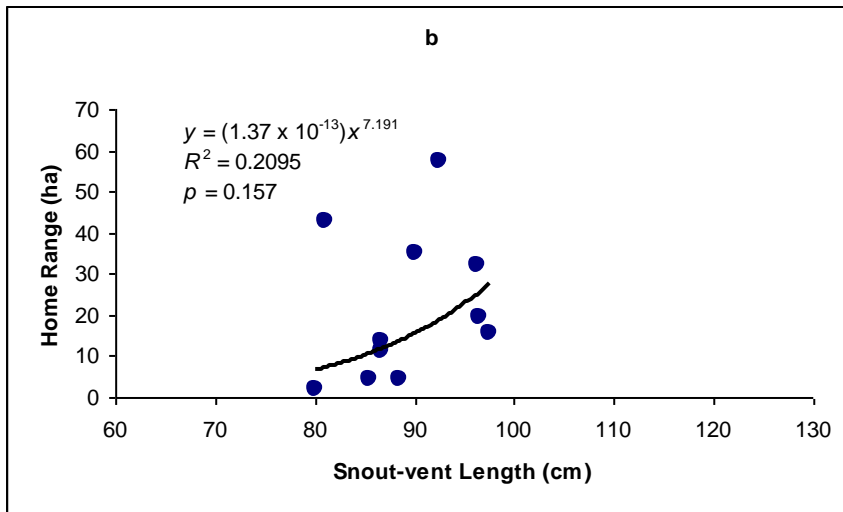
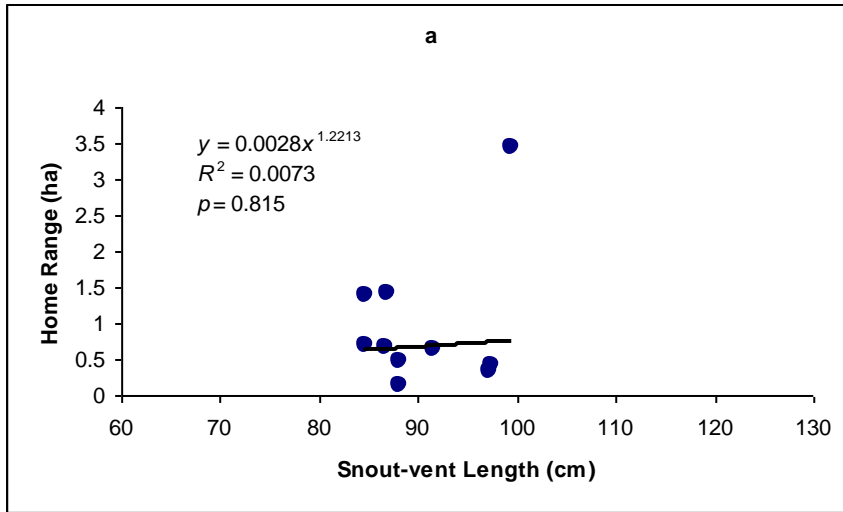




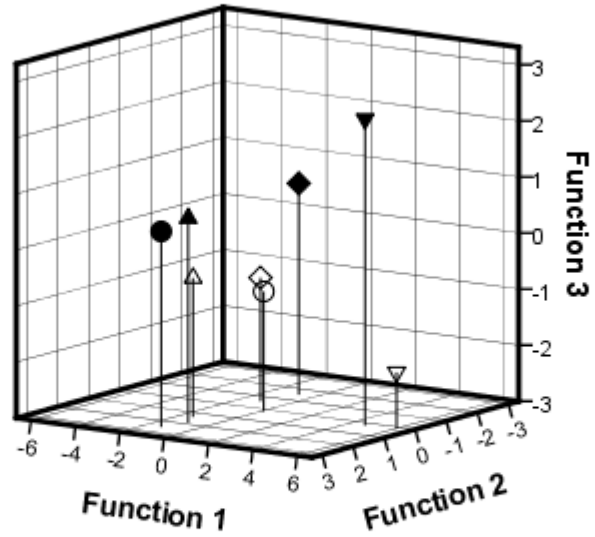
**Fig. 6.** A comparison of timber rattlesnake (*Crotalus horridus*) backtransformed activity parameters with associated 95% confidence intervals between a study from New Jersey (Reinert and Zappalorti 1988a) and the current study for: a) total distance moved, b) average daily distance moved, and c) MCP home range area.



**Fig. 7.** Examples showing the range of MCP home range overlap for three timber rattlesnakes (*Crotalus horridus*) during one active season.



**Fig. 8.** Relationship between snake snout-vent length and home range area for: a) gravid female, b) non-gravid female, and c) male timber rattlesnakes (*Crotalus horridus*).



**Fig. 9.** Plot of the first three discriminant functions describing timber rattlesnake (*Crotalus horridus*) habitat selection. Solid symbols represent the centroids for snake groups from the developed site, open symbols those from the protected natural areas. ▲ = non-gravid female ▼ = gravid female ● = male ◆ = random