The Ecology of Timber Rattlesnakes (*Crotalus horridus*) in Vermont: A First Year Progress Report Submitted to the Vermont Department of Fish and Wildlife

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Executive Summary

The timber rattlesnake (*Crotalus horridus*) has undergone extensive declines in parts of its range, particularly New England, due to habitat loss and fragmentation and human persecution. In Vermont, the timber rattlesnake is restricted to two populations in Rutland County. Although the overwintering habitat of rattlesnakes in these populations is largely protected, little is known about their population size or where these rattlesnakes move to during the summer. To address these conservation concerns, we initiated a multi-faceted study with the following objectives: 1) determine the population status of each population using mark-recapture and non-invasive surveys, 2) develop a monitoring program using these approaches to monitor changes in population status, 3) identify rattlesnake migration routes and summer foraging habitat using radio telemetry, and 4) develop a GIS tool identifying lands potentially used by rattlesnakes in each population to prioritize future land protection actions. We conducted the first year of this study in 2011 and present our results in this report. We captured and marked 104 individual rattlesnakes from one of the two populations and monitored the movements of six males with radio telemetry from May through October. We also initiated a non-invasive monitoring program at the second population using double-observer surveys to estimate rattlesnake abundance. The six telemetered rattlesnakes undertook lengthy migration from their overwintering sites, moving a mean total distance of 11.15 km and a mean of 3.46 km from their overwintering sites. On average, approximately half of each rattlesnake's home range was on protected lands. We will continue this study for a second year in 2012, during which time we will monitor additional individuals with radio telemetry. We will also continue the mark-recapture sampling and the non-invasive sampling to estimate population size and survival, and abundance, respectively. Our methods will be documented in a monitoring protocol that will be

used to monitor both populations long-term through the future. This information will be used to develop a GIS tool for prioritization land protection and conservation.

Introduction

The timber rattlesnake (*Crotalus horridus*) is one of the most widely distributed rattlesnake species in North America, historically ranging from the Atlantic Coast to the eastern edge of the Great Plains and from extreme southern Canada to the Gulf Coast (Ernst 1992, Martin et al. 2008). The timber rattlesnake has undergone extensive declines in various parts of its range (Martin et al. 2008). Although habitat loss and fragmentation remain primary threats, human persecution, often as a result of bounty hunting (Furman 2007), have contributed to declines as well (Brown 1993, Martin et al. 2008). The timber rattlesnake has declined throughout New England and is now extirpated from Maine and Rhode Island while remaining populations in Vermont, New Hampshire, and Massachusetts are few and isolated (Furman 2007, Martin et al. 2008, Clark et al. 2011). Although the timber rattlesnake is protected from direct human persecution in New England (Massachusetts DFG 2010, New Hampshire DFG 2010, Vermont NHIP 2011), and receives some protection in New York and Pennsylvania (Pennsylvania FBC 2011, New York State DEC 2011), this species is still threatened by human development. For example, timber rattlesnake hibernacula in road-fragmented landscapes were more genetically differentiated than those in contiguous landscapes, showing that the effects of habitat fragmentation can be realized in this species within seven to eight generations (Clark et al. 2010). Small populations isolated by human development are also at risk from inbreeding depression and disease (Clark et al. 2011). Timber rattlesnakes in the northeast exhibit slow, late-maturing life histories, taking up to ten years to reach sexual maturity with females reproducing every three to six years (Brown 1991, 1993, Martin 2002). Although these life history traits can help a species persist through short-term disturbances (e.g., low prey years, habitat disturbances), they also make a species sensitive to adult mortality, either natural or anthropogenic. These examples illustrate the need for conservation measures for timber rattlesnakes in New England that protect not only individual rattlesnakes but also the habitat they depend on and the landscape connecting their populations.

Populations at the climatic limits of their range are often the most at risk to population declines and extinctions because anthropogenic stressors may compound existing natural stressors. In northern and high-elevation portions of their distribution, timber rattlesnakes are faced with climatically-imposed constraints due to shorter growing seasons. This limits the amount of time available for foraging, growth, mate-searching, and gestation (Martin 2002), potentially putting these populations at greater risk from natural or anthropogenic stressors. Harsher climates also impose limits on the availability of suitable overwintering sites, which may limit the snake distributions as the requirements for suitable hibernacula become more stringent (Gregory 1984). Timber rattlesnakes in mountains regions typically overwinter at open, rocky areas with southerly aspects, yet these resources are often patchily distributed and easily fragmented (Martin 2008, Clark et al. 2010). A limitation of suitable overwintering habitat may also necessitate moving greater distances to summer foraging habitat if the two habitats are spatially separated (King and Duvall 1990). Greater numbers of conspecifics at communal hibernacula may cause individuals to travel further to locate foraging areas with fewer conspecifics (Jorgenson et al. 2008, Bauder 2010). Many populations of rattlesnakes at northerly latitudes migrate between distinct overwintering habitat and summer foraging/mating habitat (Brown 1993, Jorgenson et al. 2008). However, conserving migratory populations creates additional challenges because three habitat features must be protected: 1) overwintering habitat, 2) migration routes, and 3) summer foraging/mating habitat. Suitable gestating sites for pregnant females could also be considered another criteria (Brown 1993) as pregnant females will often seek out sunny, open areas with appropriate rocky cover during the summer and such areas may have limited availability (Reinert 1984b, Reinert and Zappalorti 1988).

Timber rattlesnakes were formerly more widespread in Vermont but now persist at only two populations and are state listed as endangered (Vermont NHIP 2011). Because small, isolated populations are at most risk from extinction, it is important to determine the size and demographics of each population. Although most of the overwintering habitat used by these populations is protected, it is unknown how much of these rattlesnakes' migration or summer habitat is protected. We initiated this study to address four primary objectives: 1) determine the population status of each population using mark-recapture and non-invasive surveys, 2) develop a monitoring program using these approaches to monitor changes in population status, 3) identify rattlesnake migration routes and summer foraging habitat using radio telemetry, and 4) develop a GIS tool identifying lands potentially used by rattlesnakes in each population to prioritize future land protection actions. An additional objective was to continue a rattlesnake removal program that was developed by The Nature Conservancy and Vermont Department of Fish and Wildlife. Under this program, landowners could contact trained individuals to remove rattlesnakes from their property. The purpose of this program was to reduce direct human-caused mortality of rattlesnakes by providing landowners that did not want rattlesnakes on their property with an alternative to killing them. In this report, we detail the results of the study's first year and describe our plans to continue meeting our project objectives.

Study Area

Our study area was Rutland County, Vermont. This area lies on the edge of the Taconic Mountains, a northern portion of the Appalachian Mountains, and is underlain by metamorphic (slate, phyllite, schist) bedrock. Vegetation communities include mesic maple-ash-hickory-oak forests and xeric oak-hickory-hophornbeam forests (Thompson and Sorenson 2005). Our study centered on the last two confirmed timber rattlesnake hibernacula complexes in the state, referred to here as Complex A and Complex B. Complex B consisted of two separate overwintering areas, B1 and B2. Each complex consists of several portals (i.e., openings) that are used by multiple rattlesnakes and are characterized by a mixture rocky soils, talus, and exposed rock outcrops.

Methods

Mark-Recapture

We searched for timber rattlesnakes at Complex A during the spring egress and fall ingress period and in the surrounding landscape during the summer. Rattlesnakes were also encountered through the rattlesnake removal program in response to calls from landowners. Each captured rattlesnake was measured (snout-vent length [SVL] and tail length), weighed, sexed by the presence of hemipenes, and marked with a Passive Integrated Transponder (PIT) tag (Biomark Inc., Boise, ID). The basal rattle segment was painted to identify recaptures and determine shedding rates and a scale clip was taken for future genetic analysis. Four individuals were not PIT-tagged due to their small size or poor body condition so their basal rattle segment was painted instead. Pregnant females were identified by palpating for embryos and the number of follicles was estimated for each pregnant female. We also made note of any skin lesions around the face and neck, as have been reported for rattlesnakes in other parts of the northeast (Clark et al. 2011, Stengle et al. 2011). All rattlesnakes were released at their capture point, unless they were part of the rattlesnake removal program, at which point they were released at the nearest protected land.

Radio Telemetry

Six male rattlesnakes captured in early May at Complex A received surgically implanted radio transmitters (9 g SI-2T transmitters, Holohil Systems Ltd., Carp, Ontario, Canada). We limited our sample size to ensure that our surgical procedures were successful and that rattlesnakes would not suffer any negative effects from the transmitters. Surgeries were conducted at a local veterinarian's office. Rattlesnakes were induced using Isoflurane and transmitters were implanted into the coloemic cavity following the procedure of Reinert and Cundall (1982). Transmitters were < 3% of the rattlesnake's body mass. Rattlesnakes were held for 24 – 48 hours following surgery to ensure recovery from anesthesia and then released at their capture site. During the summer, four rattlesnakes that were captured away from the complex were affixed with external transmitters (3.6 g R1680 transmitters, ATS, Isanti, MN). Transmitters were secured using Tegaderm™ tape (K. Michell, personal communication) and the rattlesnakes were monitored as long as possible before they moved underground for the winter. We monitored telemetered rattlesnakes from early May through mid October using a three element Yagi antenna and a R-1000 receiver (Communications Specialist, Inc., Orange, CA), locating each snake an average of once every four days. We recorded each rattlesnake's location using a handheld GPS unit (eTrex Legend or GPSMAP 62st, Garmin International, Inc., Olathe, KS). Upon locating each telemetered snake, we also recorded a brief description of its behavior and habitat.

Non-Invasive Sampling

At Complex B, we used dependent double-observer surveys (Nichols et al. 2000, Alldredge et al. 2006) to estimate rattlesnake abundance without handling or marking the rattlesnakes. Previous timber rattlesnake researchers have noted changes in the behavior (i.e., spook-factor) of marked individuals, presumably as a response to being captured and handled

(Brown 1993, 2008). As a result of this "spook-factor," we wanted to develop a non-invasive approach for monitoring the population at Complex B. Double-observer surveys allow researchers to estimate detection rates during abundance surveys (e.g., avian point counts). Two observers walk the same survey route together and each observer records the numbers of individuals detected. The data are analyzed using capture-mark-recapture models where detection by either observer is analogous to a capture/recapture event. Although some researchers use independent double-observer surveys, where each observer records their observations separately (Alldredge et al. 2006, Fletcher and Hutto 2006), we did not use this approach because we felt it would be difficult to maintain independence of observations if rattlesnakes alerted the observers to their presence by rattling. We therefore used the dependent double-observer survey where a primary observer records all individuals they detect and a secondary observer records all of the primary observer's records, as well as any individuals not detected by the primary observer (Nichols et al. 2000). Although double-observer surveys are able to estimate probability of detection given that the individual is available for detection, they cannot estimate the probability that an individual is present in the sampling area or the probability that it is available (Nichols et al. 2009, Riddle et al. 2011). For example, this approach can estimate the probability of detecting a rattlesnake that is on the surface or in crevice (i.e., available for detection) but cannot estimate the probability that a rattlesnake is on the surface or at the hibernaculum. However, we feel that estimating at least one component of detection probability will provide a better estimate of abundance than raw count data.

We implemented a trial season of the dependent double-observer approach at Complex B between September 19 and October 7. Surveys were conducted during favorable weather conditions during which we thought we could observe rattlesnakes on the surface (e.g., sunny skies and/or air temperature > 15° C). For each survey, we recorded the start and end time, the air temperature at the beginning and end of the survey, and the color phase of each rattlesnake detected (yellow or black).

Analyses

Population Ecology

We conducted a series of analyses to describe the characteristics of the population at Complex A and allow for comparisons with other studies. We compared mass, SVL, and tail length between males and females using t-tests, using only the first set of measurements made for each individual (i.e., new captures only). We also calculated a body condition index (BCI) by regressing $\log_{10}$ mass against $\log_{10}$ SVL and taking the residual (i.e., deviance from the linear trend line) as a measure of body condition (Jenkins et al. 2009). We compared mean BCI between males and females using a t-test. We used a chi-square goodness of fit test to test for an equal sex ratio, both for all new captures and for captures in the spring and fall around the portals (i.e., rattlesnakes that were just preparing to emerge or return underground). We estimated mean date of spring egress as the mean date of first capture for rattlesnakes around a portal. We concede that some individuals included in our analysis may have emerged earlier than their first capture date since, given logistical constraints and inclement weather, we were not able to search around the portals during the entire emergence period. We estimated the mean date of fall ingress as the first date an individual was captured around a portal in the fall. However, because relatively few rattlesnakes were captured around the portals, we repeated the above calculations for rattlesnakes captured at or near (< 100 m) of the portals. We recorded the number of rattlesnakes that were translocated as part of the rattlesnake removal program and the approximate distance of their translocation.

Movement Patterns

To describe rattlesnake movement patterns, we entered all telemetry locations into ArcGIS 9.3 (ESRI, Redlands, CA). We measured the straight-line distance between successive rattlesnake locations using Hawth's Tools (Beyer 2004) and summed these distances to measure total distance moved. We measured displacement for each rattlesnake as the distance of each telemetry location from the rattlesnake's capture location. To calculate movement rate, we divided the length of each movement segment by the number of days over which that movement was made (distance moved per day). We also estimated the length of each movement by calculating the mean daily movement distance. This metric was calculated identically to movement rate except that we excluded non-movements (i.e., were distance moved equaled zero) and movement distances < 5 m (King and Duvall 1990) from these calculations. We calculated a meandering ratio to measure the directionality of each rattlesnake's movements over the course of the study. The meandering ratio was calculated by dividing the maximum displacement by total distance moved and subtracting that value from one so that high values represent high meandering (Williamson and Gray 1975).

To determine if rattlesnakes in our study population were migratory, we created time series graphs of maximum displacement for each individual (Jenkins 2007, Bauder 2010). A migratory movement pattern is identified by a sharp increase in displacement, followed by one or more plateaus where displacement remains relatively constant, finally followed by a sharp decrease in displacement as the rattlesnake returns to its hibernaculum (Figure 1, Dettki and Ericsson 2008, Bauder 2010). We visually assessed each rattlesnake's graph for the presence of a migratory movement pattern. If present, we separated movements made during outbound migration from all other movements (Bauder 2010). Although we did not formally classify subsequent movements, we visually identified plateaus in displacement and refer to them as core areas in this report (Jenkins 2007, Bauder 2010). We recorded the start and end date of outbound migration and measured the distance moved during outbound migration, as well as mean movement rate and mean daily movement distance. We also measured the mean angle of outbound migration movements and the length of the mean vector for each rattlesnake (Batschelet 1981, Zar 1996). We tested if these mean angles of migration were uniformly distributed using a Rao's spacing test (Batschelet 1981, Zar 1996). All circular statistics were calculated using Oriana 2.0 (Kovach Computing Service, Pentraeth, Wales, U.K.).

We calculated home range size using multiple methods to reflect the diversity of methods previously reported in the literature. We calculated 100% minimum convex polygons (MCP) and fixed kernel utilization distributions (UD) for each rattlesnake. We retained duplicate observations (i.e., locations where rattlesnake remained for multiple days) because these observations contribute information about the intensity of space use but modified their positions by one to three meters to avoid computational difficulties. We rescaled the unit variance for each UD calculation and used a raster cell size of 10x10 m. To select the appropriate bandwidth (h) for the UD, we used two methods. We used the least-squares cross validation (LSCV, Silverman 1986, Worton 1989). However, for four out of six rattlesnakes, the LSCV function failed to find a minimum so the reference bandwidth (h_{ref}) was used instead of LSCV for each rattlesnake. For the second method, we decreased the reference bandwidth (h_{ref}) incrementally by 0.1 until we had found the bandwidth (h_{prop}) that produced the smallest contiguous polygon with no lacuna (i.e., no gaps or cavities) that included all telemetry observations (Berger and Gese 2007). For each rattlesnake's UD, we calculated 95% and 50% isopleths, representing each rattlesnake's total home range (for the duration of its tracking period) and areas of more concentrated use, respectively. All home ranges were calculated using Home Range Tools (Rodgers et al. 2007).

To evaluate the suitability of the current protected lands network around Complex A to protect rattlesnakes during the summer, we recorded the number of radio telemetry observations from the six surgically implanted rattlesnakes that were made on protected land. However, because these results are likely biased by our inability to access some private lands, we calculated the proportion of each rattlesnake's home range that fell within protected lands. We used MCP and 95% fixed kernel UD with the h_{prop} bandwidth as a conservative and liberal estimate, respectively, of home range size. We also recorded the number of non-telemetered observations (both new captures and recaptures) that were made on protected lands. To estimate the extent of protected land around each complex within a distance that was available to rattlesnakes from those complexes (available area), we buffered each complex by four kilometers, based on the greatest maximum displacement distance we observed. We clipped the area of Complex B's buffer by the state boundary, although we concede that water bodies which form the state boundary are not absolute barriers to rattlesnake movement. We then calculated the proportion of each available area that was protected. We conducted this calculation twice for Complex A, the second time clipping the available area to include only the land east of a neighboring two-lane highway (Highway X).

Results

Population Ecology

We captured and marked 104 rattlesnakes between May 7 and October 12, 2011 at Complex A and the surrounding area. Seventeen rattlesnakes were recaptured at least once during this study for a total of 24 recaptures. Twenty nine rattlesnakes were captured at or near (< 100 m) the hibernaculum in May and 34 captures were made at or near the complex in September and October. Of these 34 fall captures, only one was previously captured in the spring at the complex, one was initially captured on September 25 approximately 1.7 km south of the complex and again at the complex on October 12, and two were recaptures of rattlesnakes marked at the complex in early October. The remaining 30 fall captures were all new captures. Three rattlesnakes were captured at a birthing area just below the complex. The remaining 41 rattlesnakes were captured > 100 m from the complex. The furthest capture of a non-telemetered rattlesnake from the complex was a male captured on June 20 approximately 3.6 km from the complex. A total of eight rattlesnakes were captured > 3 km from the complex. We captured 17 neonates between September 19 and October 5. Of the 104 rattlesnakes we captured, five were yellow phase (5%). Four rattlesnakes were observed with facial lesions (4%), all between May 12 and May 27. Only one of these four individuals was recaptured (on October 8) but this individual showed no signs of facial lesions.

We captured 57 males and 39 females (1:0.68) and the difference between our observed ratio and a one-to-one ratio approached significance ($\chi^2 = 3.38$, df = 1, $p = 0.0662$). However, when we included only captures at the complex (both spring and fall), this difference was non-significant (1:0.90, $\chi^2 = 0.08$, df = 1, $p = 0.7773$). Of our 30 non-neonatal females, four were pregnant with a mean of 5.75 follicles per female. Males had significantly greater body masses than females (763 g ± 64.96 vs. 482 g ± 63.51, $p = 0.0027$) and generally had longer SVL (108.8 cm ± 17.06 vs. 75.9 cm ± 4.99, $p = 0.0684$). Males also had significantly longer tails than females (7.8 cm ± 0.36 vs. 5.4 ± 0.36, $p < 0.0001$). There was a strong relationship between $\log_{10}$ mass and log10 ($F_{1,96} = 4636.48$, $p < 0.0001$, $R^2 = 0.9797$). There was no significant difference in BCI between males and females (0.003 ± 0.011 vs. 0.000 ± 0.017, $p = 0.9044$). Mean date of spring egress was May 10 (± 0.57 days, n = 11) and mean date of fall ingress was October 7 (± 15.70 days, n = 8) for rattlesnakes captured around portals. When rattlesnakes captured near (<

100 m) the complex were included, mean date of spring egress was May 12 (± 0.59 days) and mean date of fall ingress was October 2 (± 1.41 days). Only two rattlesnakes were translocated as part of the rattlesnake removal program, both males. One male was moved approximately 1.24 km NE onto protected land. The translocation distance was not recorded for the second snake but was comparable to that of the first. Another landowner called about removing a third rattlesnake but was unable to reach anyone in the rattlesnake removal program at that time to remove the rattlesnake. Another person contacted us about a fourth rattlesnake, although this individual did not want the rattlesnake removed. As a result of this contact, we were able to catch the rattlesnake and affix it with an external transmitter.

Movement Patterns

The six rattlesnakes with surgically implanted radio transmitters were monitored from their capture at Complex A in early to May to their return to the complex in early October (May 13, 2011 and October 12, 2011). Mean SVL of these telemetered rattlesnakes was 113 cm (± 4.68) and mean mass was 1,020 g (± 91.36). Each snake was located approximately 35 times (± 2.17). One individual (CH001) moved onto private property for which we did not have permission to access. Of the four rattlesnakes that were affixed with external transmitters, three were not located again during 2011 because the purpose of those transmitters was to locate the rattlesnakes again the following spring. Two of these individuals were captured near Complex A in early October and a third was captured on September 19 approximately 875 m from the complex. Two of these three individuals were yellow-phase rattlesnakes. The fourth individual fitted with an external transmitter was captured August 5, 2011 approximately 611 m north of Complex A on private property as part of the rattlesnake removal program. This individual proceeded to move in a southerly direction towards Complex A and was approximately 200 m east of the complex when her transmitter was removed due to issues with the Tegaderm® tape. We report on the results from the six telemetered rattlesnakes with surgically implanted transmitters in subsequent sections.

These six telemetered rattlesnakes moved a mean total distance of 11.15 km (± 1.03) and had a mean maximum displacement of 3.46 km (± 0.14, Table 1). Mean meandering ratio was 0.68 (± 0.03). Home range size varied depending on the calculation method used (Table 2). The 95% fixed kernel UD with h_{ref} produced the largest estimates (mean = 925.20 ha ± 573.40), followed by the 95% fixed kernel UD with h_{prop} (mean = 519.89 ha ± 406.97), and finally the MCP (257.96 ha ± 356.03). Activity area size (i.e., 50% fixed kernel UD) varied similarly by bandwidth (h_{ref}: mean = 224.09 ha ± 157.85, h_{prop} = 114.89 ha ± 106.96). Several rattlesnakes showed multiple areas of concentrated use (i.e., 50% fixed kernel UD), and the number of these areas depended on the bandwidth used (h_{ref}: mean = 1.50 ± 1.34, h_{prop} = 1.67 ± 1.26).

The six rattlesnakes we monitored were highly migratory, undertaking a series of lengthy and linear movements away from Complex A following their emergence in the spring and then returning to the complex in the fall (Figure 2). The mean angle of outbound migration was 70.08° (± 17.19°) with a 95% confidence interval of 36.39° - 103.79° (Figure 3). The distribution of migration bearings was significantly non-uniform ($U = 207.91$, $p < 0.01$). The mean length of outbound migrations was 3.09 km (± 0.17) while the mean meandering ratio was 0.11 (± 0.04). Another measure of linearity, the length of the mean vector, also indicated very linear movement (mean = 0.92 ± 0.01, range = 0.89 – 0.95). Outbound migration movements were few in number (mean = 6.17 ± 0.75) but were rapid (mean daily movement length = 163.87 m/day ± 22.37). The initial series of movements away from the complex were very consistent in timing, beginning by May 23 (i.e., within eleven days following release) and ending by June 7. Cessation of the initial migration was followed by a series of shorter, less directional movements which represent a summer core area (Figures 4A - 4F). For two rattlesnakes (CH004 and CH024), this change in movement patterns was associated with ecdysis. Four individuals maintained fairly discrete summer core areas (Figures 4C, 4D, 4E, and 4F). CH004 engaged in lengthy and rapid movements throughout the summer but these movements had low directionality (Figure 4B). We did not have sufficient data to determine the shape or extent of CH001's summer core area. All individuals undertook movements back to Complex A in late summer or fall that were very similar in nature to their initial outbound migration. Inbound migration closely followed the direction and route of outbound migration. Although one individual (CH024), appeared to begin inbound migration in July, all other inbound migrations occurred primarily during late August and September.

Fifty four percent of all telemetry observations occurred on protected lands. The majority of these observations (55%) were centered on protected lands that include most of Complex A. These percentages were very similar to the mean percentage of home range that fell within protected lands (50% for MCP and 53% for 95% fixed kernel UD). However, these mean values had very high standard errors (0.61 and 0.48, respectively), indicating a large amount of individual variability. The vast majority of non-telemetered rattlesnake captures were on protected lands (91%), primarily because most of these captures were made at Complex A. Approximately 70% of the area available to rattlesnakes around Complex B was protected land. In contrast, only 36% of the area available to rattlesnakes from Complex A is protected. This percentage only increases to 40% when the area west of Highway X is removed.

Non-Invasive Sampling

We conducted total of nine surveys at Complex B, five surveys at Complex B1 and four at Complex B2. During each survey, the secondary observer detected rattlesnakes that were not detected by the primary observer. The primary observer detected a mean of 5.6 rattlesnakes (± 2.06) per survey at Complex B1 and a mean of 1.0 rattlesnake (± 0.41) per survey at Complex B2. The secondary observer detected a mean of 1.6 rattlesnakes (± 0.60) per survey at Complex B1 and a mean of 0.75 rattlesnakes (± 0.45) at Complex B2. A total of 36 rattlesnakes were detected at Complex B1 and seven at Complex B2. The secondary observer increased the number of rattlesnakes detected by a mean of 32% (± 0.50) per survey at Complex B1 and 14% (± 0.29) per survey at Complex B2.

Discussion

Complex A apparently supports a relatively robust population of timber rattlesnakes. Although we are unable to estimate population size with the data we have, our results suggest that the population may exceed 100 individuals. Although only 60 individuals were captured around the portals, it is likely that most of the 44 individuals captured away from the complex during the summer also utilized Complex A. However, four individuals (one marked, CH099) were around the opening of a new portal. Additional monitoring of both marked and radio telemetered individuals may confirm the presence of additional portals within and around Complex A and allow us to determine the numbers of rattlesnakes using these complexes. Egress and ingress times were similar to those reported by Brown (1992) in northeastern New York and by Martin (2002) at a high elevation (1075 m) site in West Virginia, although our mean dates of ingress were slightly later. Activity seasons were longer for timber rattlesnakes at lower elevations (200 – 400 m) in northwest Virginia (Martin 1992).We observed 30 neonates associated with Complex A in the fall indicating successful reproduction this year. Although our observed sex ratio from all captures was significantly male-biased, this could be the result of greater male activity during the summer. Males are known to move further than females during the summer, primarily because of male mate-searching, and thus may be encountered more frequently than females during the summer (Brown 1993, Waldron et al. 2006). A male-biased sex ratio may also suggest lower female survivorship, which is consistent with the increased stress placed on females to acquire enough resources for reproduction and their increased vulnerability during pregnancy (Brown 1993). However, the equal sex ratio we observed around the portals in the spring and fall may suggest that differential mortality may not be the cause of our male-biased sex ratio using all captures. Although we do not have direct estimates of mean litter size, the mean number of follicles per gravid female was 5.75. This value is lower than values reported for timber rattlesnakes in northeastern New York (Brown 1993), although our low sample size for pregnant females may have also contributed to this difference.

Very few individuals were observed with the facial lesions that were reported for timber rattlesnakes in New England (Clark et al. 2011, Stengle et al. 2011). Furthermore, all lesions we observed were in the spring and no lesions were observed on rattlesnakes captured during the summer and fall. These observations, as well as the observation that one individual in our study recovered from its lesions, suggest that facial skin lesions may not be a serious threat to rattlesnake populations in Vermont.

The migratory movement patterns of timber rattlesnakes in our study were consistent with what has been reported from other timber rattlesnake studies (Brown 1993, Martin et al. 2008). Although a trend may exist for timber rattlesnakes at northern latitudes to migrate further than timber rattlesnakes at southern latitudes (Martin et al. 2008), the maximum displacement distances observed in our study were generally greater than those reported from timber rattlesnakes in the northeast. Timber rattlesnakes in our study generally moved greater distances, both total distance and maximum displacement, than those reported for male timber rattlesnakes in Pennsylvania (Reinert et al. 2011b), New Jersey (Reinert and Zappalorti 1988), and the Allegheny Plateau of West Virginia (Martin 2002). Home range sizes in Vermont were also larger than those in Pennsylvania (Brown 1993). However, Martin (1992) recorded a migration distance of six kilometers from a timber rattlesnake in the Appalachian Mountains in Virginia. In northeastern New York, Brown (1993) observed a mean maximum migration distance (mean of the five longest migrations) for male timber rattlesnakes of 4.07 km and a maximum migratory movement of 7.2 km. The greatest maximum displacement in our study was 4.08 km (CH001). The reasons behind the more extensive movements in our study are unknown and may include a greater spatial separation between winter and summer habitat, more patchily distributed small mammal prey, and/or attempts to locate foraging locations away from the presence of conspecifics (Jorgenson et al. 2008, Bauder 2010). Previous timber rattlesnake researchers have not distinguished between migratory and foraging/mate searching movements (but see Waldron et al. 2006), making it difficult to directly compare the characteristics of our migration movements. However, our results are very similar to those obtained for prairie and western rattlesnakes (*Crotalus viridis* and *C. oreganus*) in western North America (Jorgenson et al. 2008). These species undertake very linear migrations (length of mean vector 0.61 – 0.93, Cobb 1994, King and Duvall 1990, Bauder 2010) from their hibernacula that can extend up to 4.8 km (Cobb 1994). Prairie rattlesnakes in southern Canada have moved over 20 km from their hibernacula during migration (Didiuk 1999). The migratory movements, as well as total distance moved and maximum displacement, observed in our study were still greater than most reported for prairie and western rattlesnakes (Jorgenson et al. 2008).

The behavior of our telemetered rattlesnakes varied after their initial outbound migration ceased. Establishment of summer core areas is typically associated with foraging and shedding behavior (Bauder 2010) and this appeared to be the case in our study. We made multiple observations of individuals in ambush foraging postures (Figure 5, Reinert et al. 1984, 2011a) while within their core areas. There did not appear to be any strong association with habitat type during the summer as rattlesnakes were observed in deciduous forests, coniferous forests, mixed forests, edges of cultivated land, and forested wetlands. Most telemetry observations were in deciduous forests, reflecting this habitat's greater availability and the foraging habits of the timber rattlesnake (Reinert 1984a, 1984b, Reinert et al. 1984). Some individuals seemed to show greater use of a particular habitat feature, such as wetland or field edges. Two individuals (CH001 and CH024) may have continued their outbound migration after their initial pause in early June by continuing to a second core area. Additionally, some individuals appeared to exhibit additional extensive movements in July and August, which were likely associated with mate searching (Aldridge and Brown 1995, Waldron et al. 2006). These movements were often rapid and lengthy but had very low directionality, a pattern that was also observed by male prairie rattlesnakes (Bauder 2010). One individual (CH004) undertook very extensive movements during July – September that resembled mate searching movements in their length and lack of directionality (Bauder 2010). This individual was observed mating with a female and it is possible that he spent most of the year searching for females as such behavior was apparently observed in western rattlesnakes (Jenkins and Peterson 2006).

The current network of protected lands surrounding Complex A appears to protect a substantial amount of timber rattlesnake migration and summer foraging/mate searching habitat. However, the majority of the area that is theoretically available to rattlesnakes from Complex A on both sides of Highway X is unprotected. Rattlesnakes that move roughly east of the Complex A are offered the greatest protection because most protected lands are in this direction. However, half of our telemetered rattlesnakes migrated in a northeasterly direction and spent the majority of the summer on private land. One striking result of our study was that all of our telemetered rattlesnakes migrating away from or parallel to Highway X. Dead rattlesnakes are occasionally observed on Highway X (DB and KVB, unpublished data) and it is possible that the highway represents a barrier to rattlesnake movement. Roads are known to cause genetic isolation among rattlesnake hibernacula in the northeast (Clark et al. 2010). With our small sample size, we cannot say that rattlesnakes from Complex A do not successfully migrate across Highway X, although all six telemetered rattlesnakes in this study migrated away from the highway. However, additional radio telemetry may show that some individuals continue to migrate across the highway. In order to restore or enhance rattlesnake migrations across the highway, wildlife crossing structures, such as culverts, could be employed to reduce road mortality.

Although we have not yet derived abundance estimates for the populations at Complex B, this complex still appears to support a fairly robust population of timber rattlesnakes, although the numbers we observed were smaller than those observed at Complex A. Previous anecdotal observations of timber rattlesnake numbers during egress and ingress are consistent with the numbers we observed (DB and KVB, unpublished data). One interesting result of our pilot non-invasive surveys as that including a secondary observer increased our detection rates. Although we are unable to estimate all components of detection rate using a double-observer approach, our results show that a single observer does not detect all rattlesnakes that are on the surface and available for detection. As we collect additional data using this approach, we will estimate detection rates and correct our raw counts using our detection rate. This will allow us to quantify the increase in abundance that we obtain by including a second observer.

Plans for Future Research

This report describes the results from the first year of this study. We will continue and expand this study in 2012 by continuing the mark-recapture monitoring at Complex A. With two years of data we will be able to obtain preliminary estimates of survival and population size. However, we caution that mark-recapture studies require several years of data to obtain reliable and precise estimates of population parameters. We will continue our non-invasive surveys at Complex B and generate abundance estimates based on our dependent double-observer surveys. We will also expand our radio telemetry efforts by tracking approximately 20 individuals at Complex A in 2012, including non-pregnant females. A larger sample size will allow us to identify other areas used for migration, summer foraging/mate searching, and gestation. It may also allow us to determine if any rattlesnakes are attempting to cross Highway X and what areas west of the highway are used as summer habitat. A more detailed and extensive data set will allow us to develop a more accurate GIS tool for prioritizing land protection and conservation. It will also increase in the precision of our population ecology, movement, and home range estimates, allowing for a better comparison with other timber rattlesnake studies. We will also continue the rattlesnake removal program and will modify the program to increase our response rate, as we were unable to respond to one of the calls received. At the conclusion of the 2012 field season, we will begin developing the GIS tool and preparing a final report and publication of this study. We will then implement the mark-recapture and non-invasive monitoring protocols at their respective hibernacula to allow for long-term monitoring of those populations. This long-term monitoring will be conducted by Vermont Fish and Wildlife.

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Tables and Figures

Table 1. Annual movement statistics for six male timber rattlesnakes (*Crotalus horridus*) monitored with radio telemetry May – October 2011 in west-central Vermont.

Snake ID	Mass (g)	SVL (cm)	No. of locations	Location interval (days)	Total distance moved (km)	Maximum displacement (km)	Meandering Ratio
CH001	1100	118	26	5.96	11.06	4.08	0.63
CH004	840	104	41	3.73	15.56	3.52	0.77
CH007	1150	118	33	4.45	9.78	3.40	0.65
CH009	1190	121	37	4.08	11.42	3.37	0.71
CH023	1190	121	38	3.92	11.22	2.99	0.73
CH024	650	93	32	4.90	7.90	3.43	0.57
Mean	1020	113	35	4.51	11.15	3.46	0.68
SE	91.36	4.68	2.17	0.34	1.03	0.14	0.03

Table 2. Annual home range sizes for six male timber rattlesnakes (*Crotalus horridus*) monitored with radio telemetry May – October 2011 in west-central Vermont. MCP = minimum convex polygon. Prop of h_{ref} = proportion of the reference bandwidth used to select the bandwidth for the h_{prop} 95% and 50% fixed kernel UD, following Berger and Gese (2007). No. of activity centers = number of distinct polygons generated with the 50% fixed kernel UD.

Snake ID	MCP (ha)	Prop. of h_{ref}	95% UD h_{prop} (ha)	50% UD h_{prop} (ha)	No. activity centers h_{prop}	95% UD h_{ref} (ha)	50% UD h_{ref} (ha)	No. activity centers h_{ref}
CH001	377.90	0.5	622.62	153.51	2	1245.58	325.77	1
CH004	489.36	0.7	690.42	152.28	1	973.44	213.62	1
CH007	123.28	0.7	688.03	155.95	2	1106.13	269.25	2
CH009	186.42	0.4	425.61	90.43	1	889.40	205.78	1
CH023	229.62	0.6	368.44	64.99	2	629.35	143.04	2
CH024	141.16	0.5	324.21	72.20	2	707.31	187.06	2
Mean	257.96		519.89	114.89	1.67	925.20	224.09	1.50
SE	356.03		406.97	106.96	1.26	573.40	157.85	1.34

Table 3. Outbound migration movement statistics for six male timber rattlesnakes (*Crotalus horridus*) monitored with radio telemetry May – October 2011 in west-central Vermont. Mean daily movement distance is calculated the same way as daily movement rate except that non-movements (i.e., days the rattlesnake did not move) were excluded. Movement rate and mean daily movement distance were identical during migration. Post-migration movement rate and mean daily movement distance were calculated using all movement data following the end of outbound migration.

Snake ID	No. of movements	Days spent in migration	Migration length (km)	Meandering ratio during migration	Movement rate, migration (m/day)	Post-migration movement rate (m/day)	Mean daily movement distance, post-migration (m/day)
CH001	8	28	2.91	0.09	103.97	100.02	105.87
CH004	7	20	3.45	0.11	173.54	133.36	137.41
CH007	4	11	3.43	0.29	245.12	48.92	55.64
CH009	6	14	3.39	0.07	207.24	67.35	72.16
CH023	8	18	2.93	0.07	132.98	70.13	87.63
CH024	4	20	2.42	0.04	120.38	38.65	49.51
Mean	6.17	18.50	3.09	0.11	163.87	76.41	84.70
SE	0.75	2.39	0.17	0.04	22.37	14.26	13.51

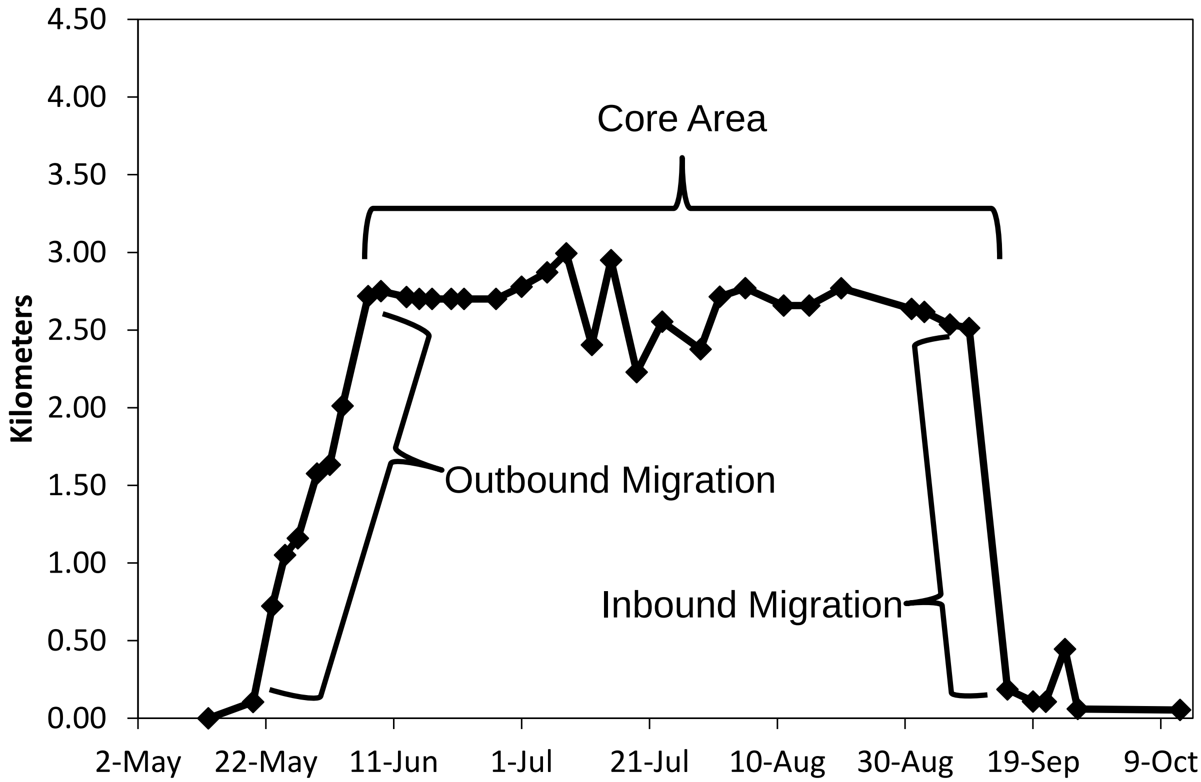

Figure 1. An example of a time series of displacement for a radio telemetered timber rattlesnake (*Crotalus horridus*) from west-central Vermont showing how migration and core area movements were visually identified. Outbound migration was defined as a series of long, rapid movements away from the hibernaculum, core areas were defined as periods of slower, shorter movements at a relatively stable distance from the hibernaculum, and inbound migration was defined as a series of long, rapid movements back towards the hibernaculum.

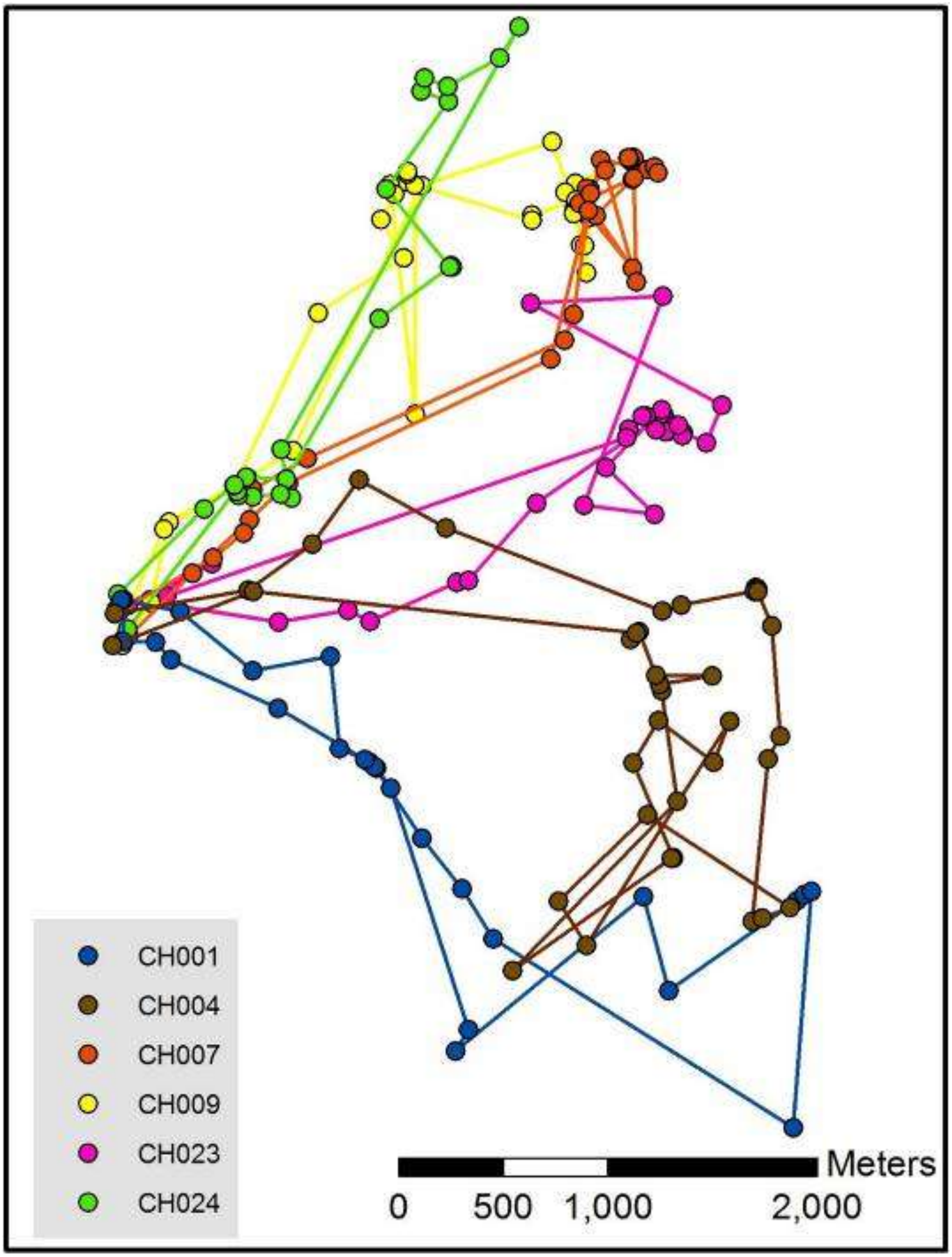

Figure 2. Movement patterns for six male timber rattlesnakes (*Crotalus horridus*) monitored with radio telemetry in west-central Vermont May – October 2011.

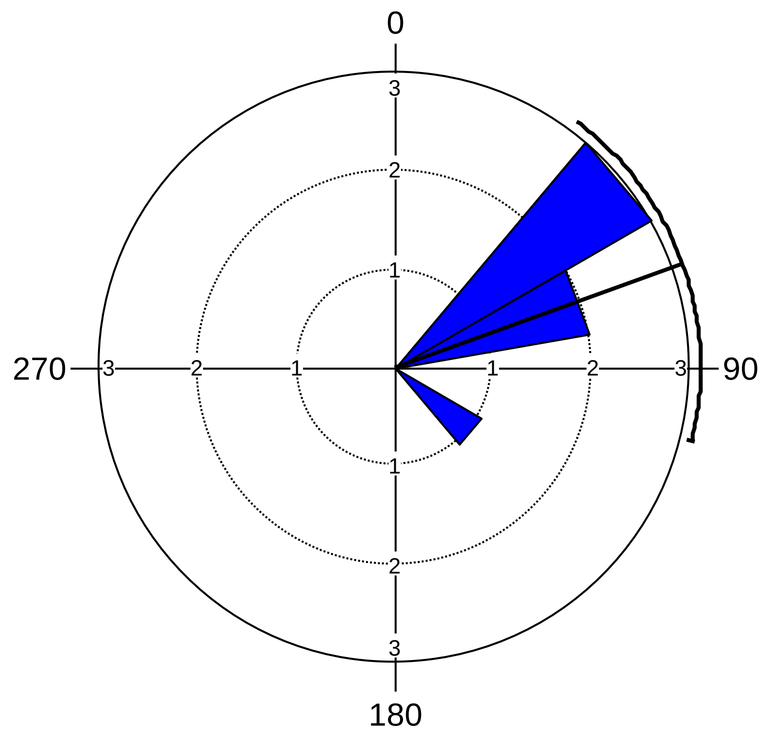

Figure 3. Circular histogram showing the mean bearing of outbound migration for six male timber rattlesnakes (*Crotalus horridus*) monitored with radio telemetry May – October 2011 in west-central Vermont. The mean bearing and 95% confidence interval are indicated by the black lines.

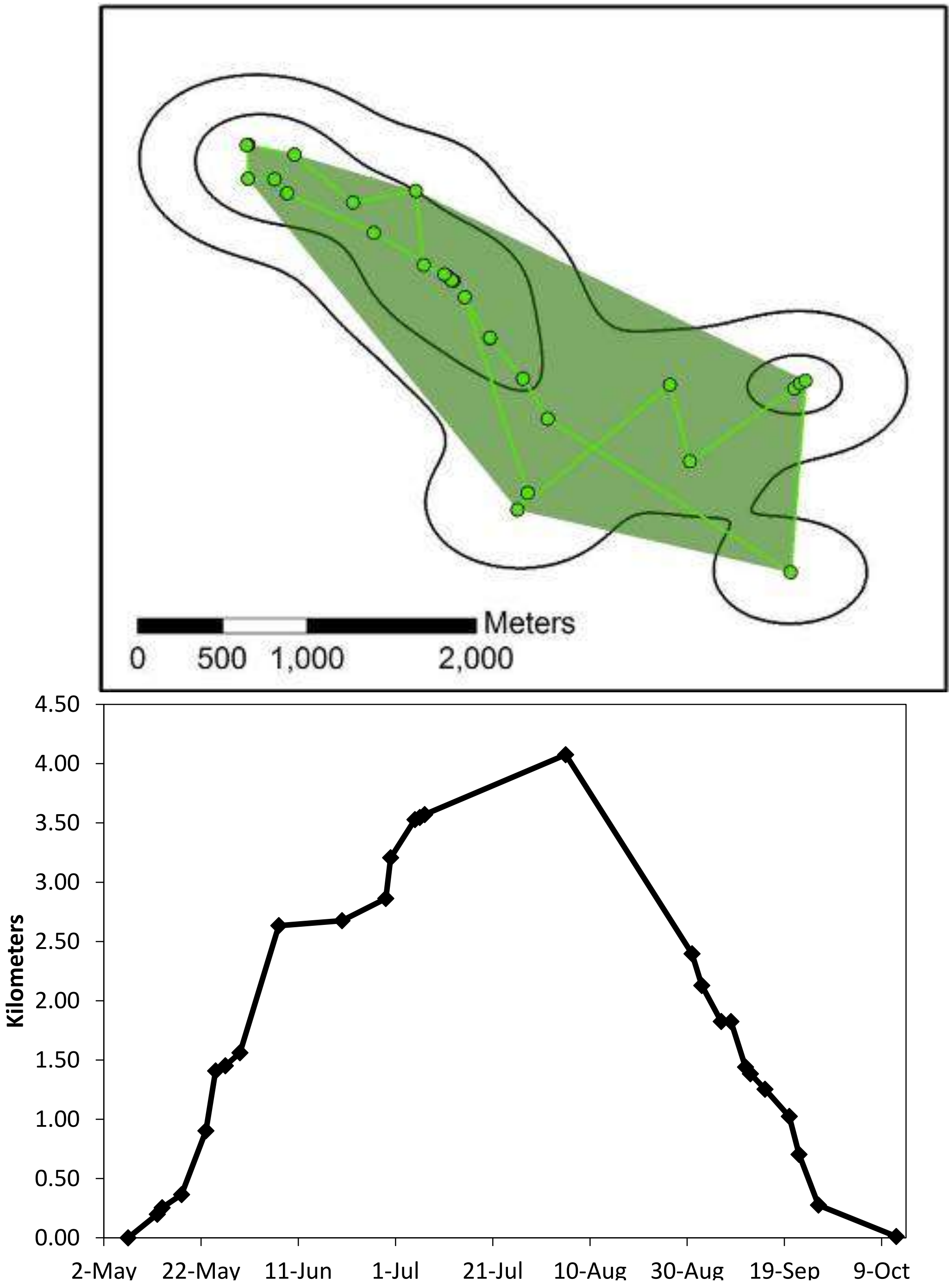

Figure 4A. Movement patterns for radio telemetered timber rattlesnake (*Crotalus horridus*) CH001 in west-central Vermont, May – October 2011. Top panel shows the telemetry locations, movement pathway, minimum convex polygon home range (green shaded), and 95% and 50% fixed kernel UD (inner and outer polygons, respectively).

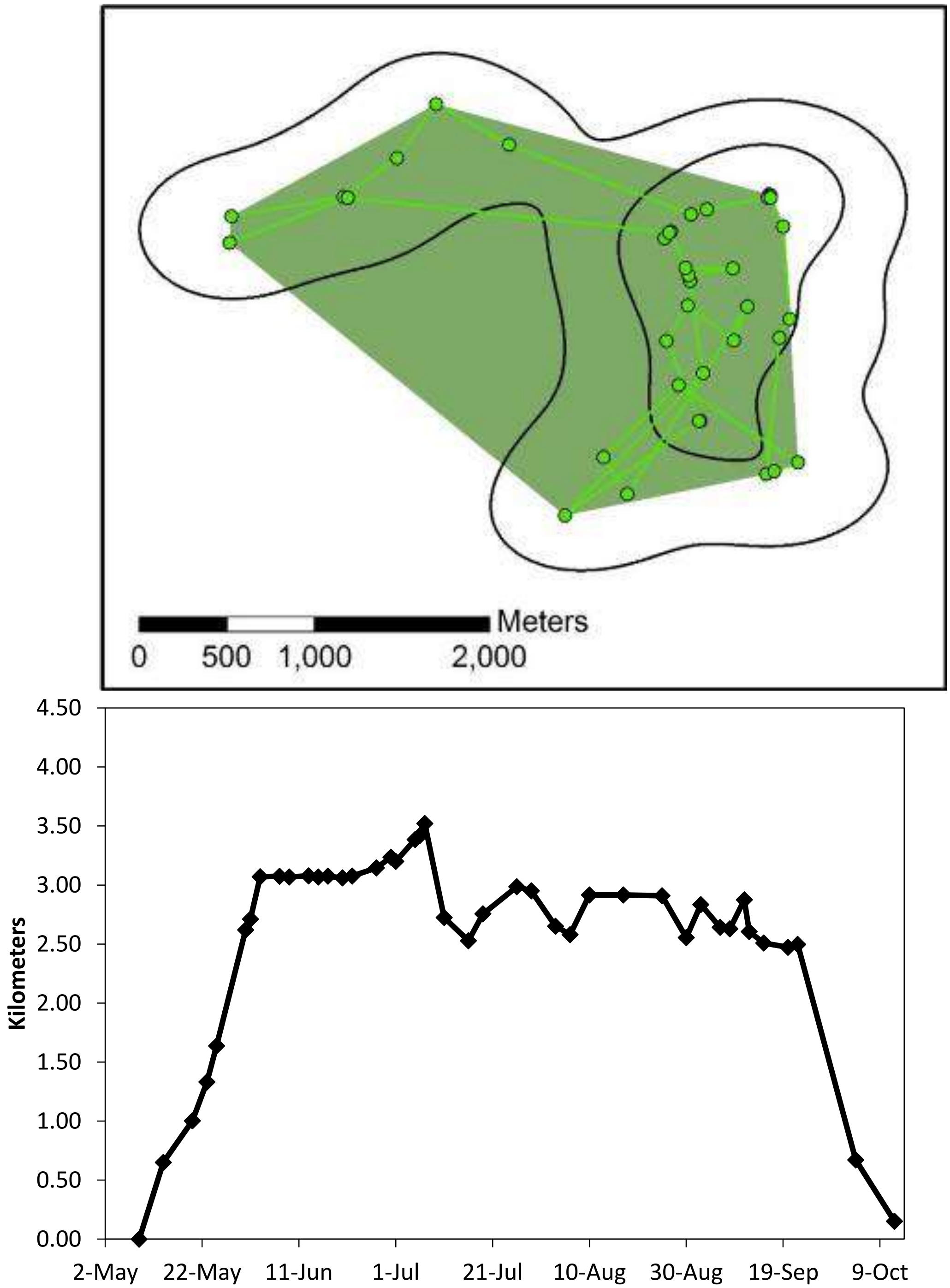

Figure 4B. Movement patterns for radio telemetered timber rattlesnake (*Crotalus horridus*) CH004 in west-central Vermont, May – October 2011. Top panel shows the telemetry locations, movement pathway, minimum convex polygon home range (green shaded), and 95% and 50% fixed kernel UD (inner and outer polygons, respectively).

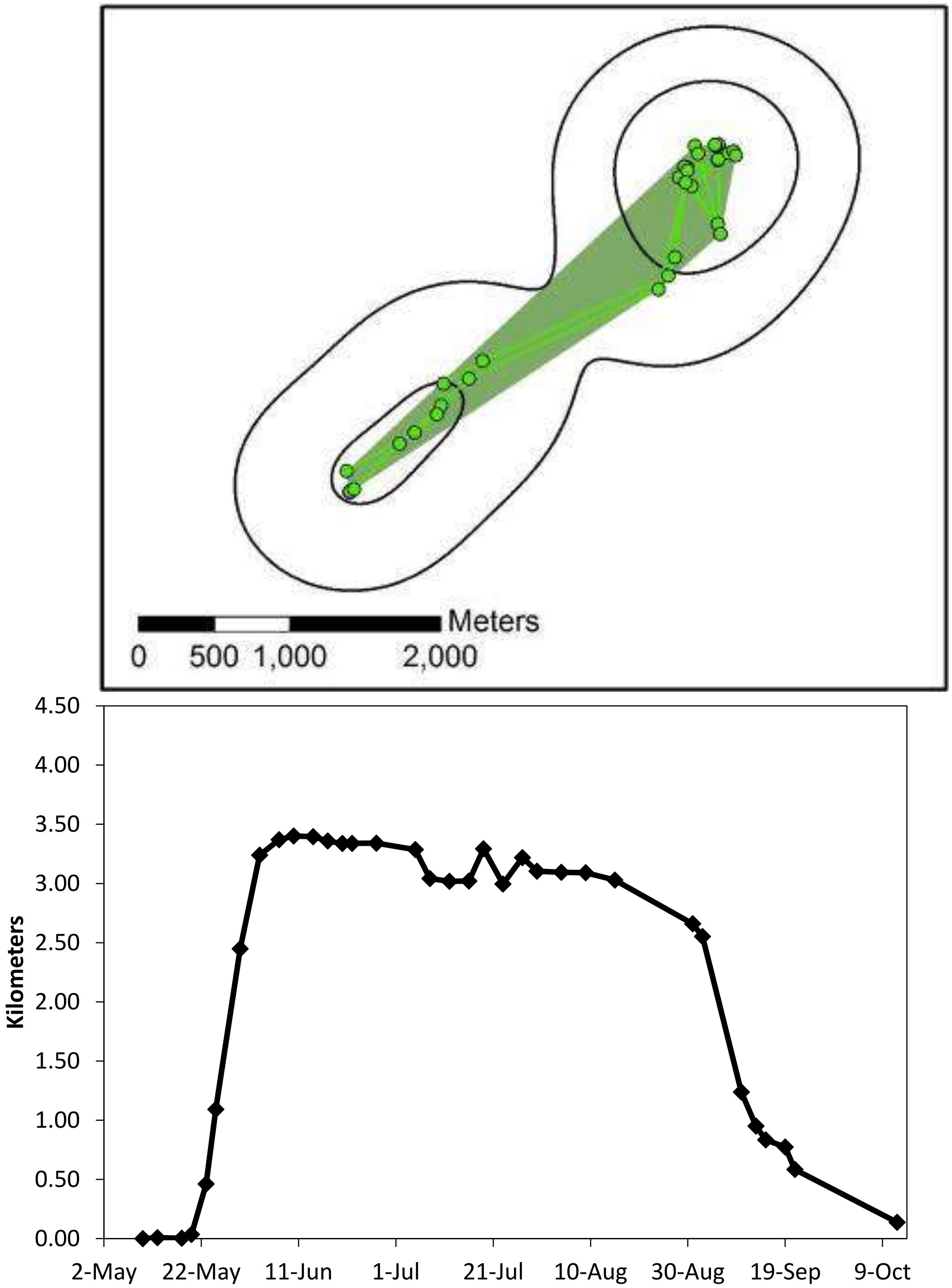

Figure 4C. Movement patterns for radio telemetered timber rattlesnake (*Crotalus horridus*) CH007 in west-central Vermont, May – October 2011. Top panel shows the telemetry locations, movement pathway, minimum convex polygon home range (green shaded), and 95% and 50% fixed kernel UD (inner and outer polygons, respectively).

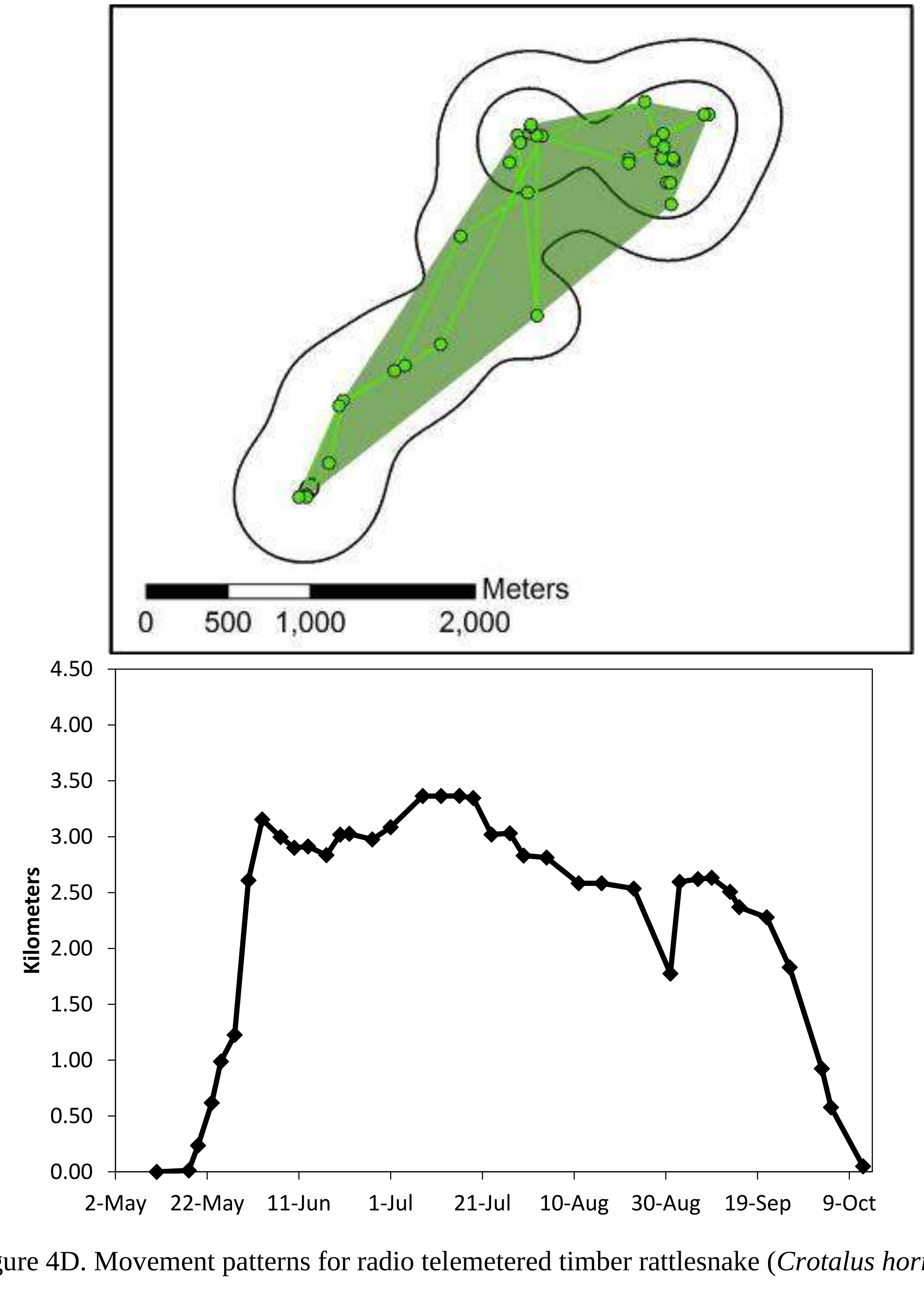

Figure 4D. Movement patterns for radio telemetered timber rattlesnake (*Crotalus horridus*) CH009 in west-central Vermont, May – October 2011. Top panel shows the telemetry locations, movement pathway, minimum convex polygon home range (green shaded), and 95% and 50% fixed kernel UD (inner and outer polygons, respectively).

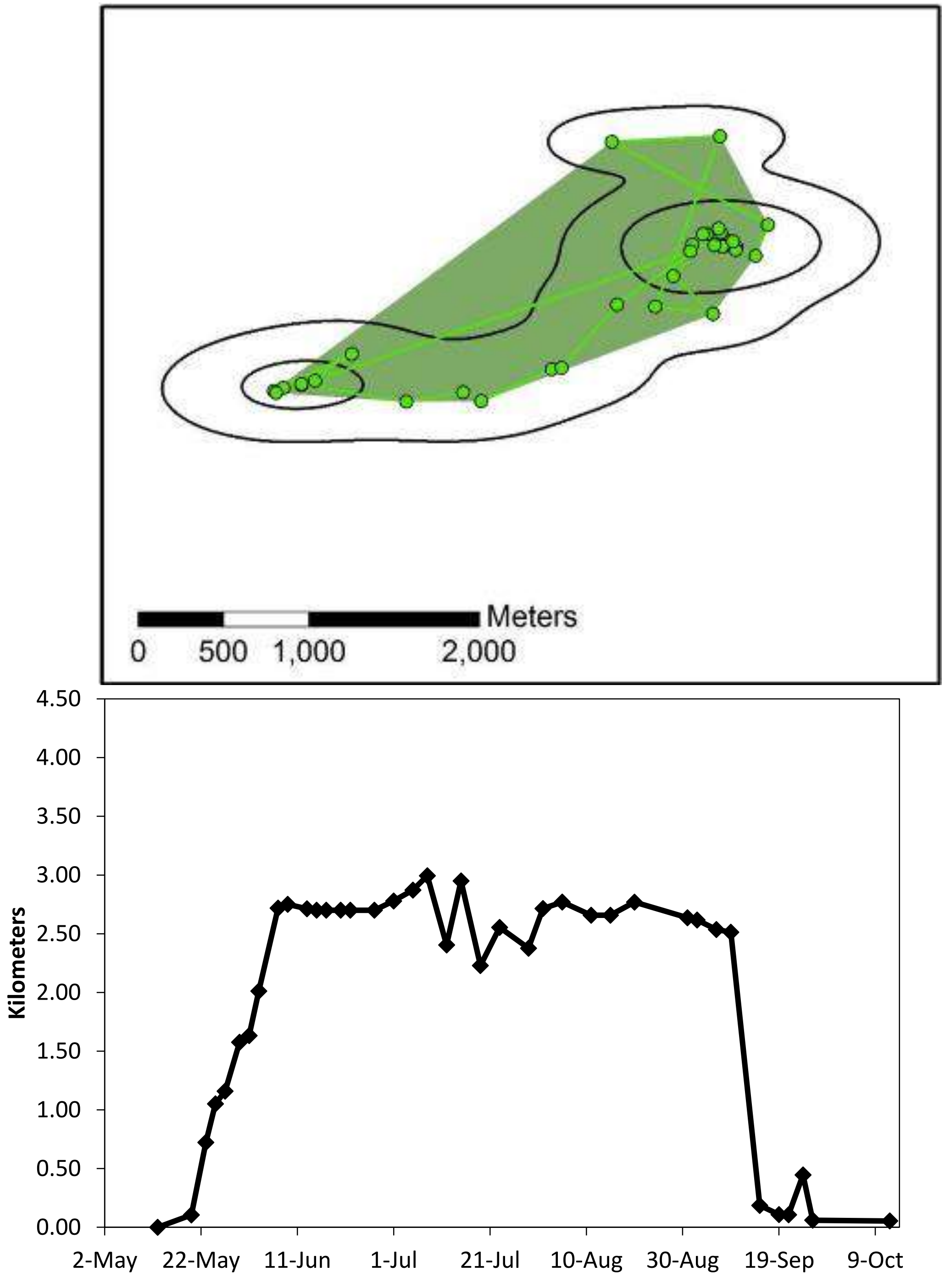

Figure 4E. Movement patterns for radio telemetered timber rattlesnake (*Crotalus horridus*) CH023 in west-central Vermont, May – October 2011. Top panel shows the telemetry locations, movement pathway, minimum convex polygon home range (green shaded), and 95% and 50% fixed kernel UD (inner and outer polygons, respectively).

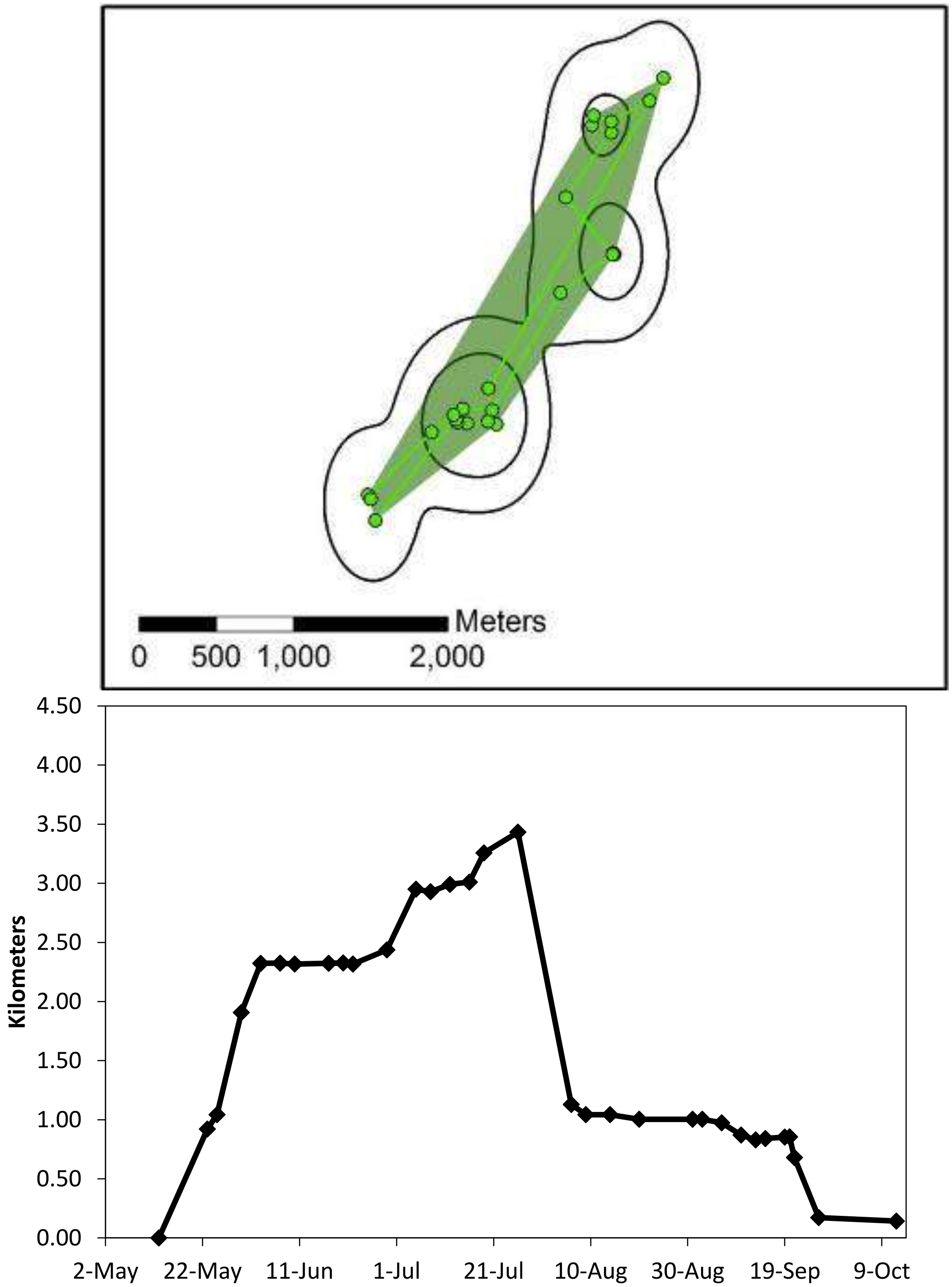

Figure 4F. Movement patterns for radio telemetered timber rattlesnake (*Crotalus horridus*) CH024 in west-central Vermont, May – October 2011. Top panel shows the telemetry locations, movement pathway, minimum convex polygon home range (green shaded), and 95% and 50% fixed kernel UD (inner and outer polygons, respectively).

Figure 5. An example of a timber rattlesnake (*Crotalus horridus*) from west-central Vermont in an ambush foraging posture, as described by Reinert et al. (1984, 2011a). Photo by Kiley V. Briggs.