

THE SPATIAL AND REPRODUCTIVE ECOLOGY OF THE COPPERHEAD (*AGKISTRODON CONTORTRIX*) AT THE NORTHEASTERN EXTREME OF ITS RANGE

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ABSTRACT: We studied the spatial and reproductive ecology of a population of Copperheads (*Agkistrodon contortrix*), a North American pitviper, in a basalt trap-rock ecosystem in the central Connecticut River Valley, a region that constitutes the northeastern extreme of this species' geographic range. Adult males ($n = 20$) and females ($n = 15$) were surgically implanted with radio-transmitters and tracked every 48 h during the active season (April through October) for three consecutive years (2001 to 2003). From late autumn to early spring (November through March), when snakes were hibernating and thus inactive, tracking was reduced to once per week. We generated data on movement and other spatial parameters for each subject using GPS coordinates. There were significant sex differences in activity range size and multiple movement parameters. Throughout the active season males had greater activity range sizes and showed greater movement than females. This trend was pronounced during the mating season, which was restricted to late summer and early fall (late July through September). In contrast to most populations of *A. contortrix* from more southern and western localities, we did not observe any sexual activity (e.g., courtship, coitus, and male–male fighting) in the spring. Individuals of both sexes showed annual fidelity to: (i) activity range location, (ii) activity range size, (iii) movement distances, (iv) particular features of their activity ranges (e.g., refuge sites), and (v) hibernation sites. Males and females showed no difference in preferred seasonal habitats. In both sexes, shifts in habitat associations during the active season included migrations from over-wintering sites within basalt trap rockslides to upper-elevation, open deciduous forest during the summer foraging and reproductive season. Parturition in the field was recorded in eight instances and was always close to one of the two hibernacula used by the individuals in the study area.

Key words: Activity range; *Agkistrodon*; Geographic variation; Mating system; Migration; Movement; Reproduction; Reptile; Snakes.

A CENTRAL prediction of evolutionary theory is that species with extensive distributions differ geographically in a wide range of phenotypic characteristics (traits), presumably as a result of adaptive responses to local environments (Boake et al., 2002; Darwin, 1859; Endler, 1977, 1986; Roff, 2002; Stearns, 1992). Moreover, these differences are often pronounced at range edges (Bahn et al., 2006; Holt and Keitt, 2005). In terrestrial taxa, for example, such geographical variation includes morphology (Ashton, 2001, 2004; Lyberth et al., 2007; Manier et al., 2007), life history (Roff, 2002; Shine, 2005; Stearns, 1992), social and spatial structure (Jones and Reichert, 2008; Lott, 1991; Shuster and Wade, 2003), and reproduction, such as seasonal timing of

mating (Aldridge and Duvall, 2002; Schuett, 1992).

Compared to other vertebrates, of the approximately 3000 species of extant snakes (Greene, 1997), detailed knowledge of spatial ecology and reproduction are limited to only a handful of taxa (e.g., Blouin-Demers et al., 2005; Duvall et al., 1992, 1993; Gibbs and Weatherhead, 2001; Madsen and Shine, 1992; Madsen et al., 1993; Shine, 2003; Weatherhead et al., 1995), and few comparative data are available on species that have expansive geographic distributions (see Graham et al., 2008; Shine and Fitzgerald, 1995). Even in well-studied species of snakes, the period of breeding (mating season) is often poorly understood (Graham et al., 2008; Schuett, 1992; Schuett et al., 2002, 2005; Shine, 2003). This is not a trivial point; for example, interpreting reproductive success in males

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and females hinges on knowing the seasonal timing and duration of the mating season (Andersson, 1994; Duvall et al., 1992, 1993; Shuster and Wade, 2003). Consequently, the degree to which local environments influence use of space and reproductive activities of snakes is a rich area for future studies (Aldridge and Duvall, 2002; Duvall et al., 1993; Seigel and Ford, 2001; Shine, 2003, 2005).

Through the use of radio-telemetry for three consecutive years (2001–2003), we addressed multiple questions pertaining to the spatial and reproductive ecology of a population of the Copperhead (*Agkistrodon contortrix*)—a common, medium-sized North American pitviper—at the northeastern extreme of its extensive geographic range (Campbell and Lamar, 2004; Douglas et al., 2009; Gloyd and Conant, 1990). Specifically, we investigated: (i) movements and space use among years; (ii) sex differences in movements and space use; (iii) fidelity to sites used at different times across seasons, including hibernacula; (iv) seasonal timing and duration of the mating season; and (v) timing of birth and location of parturition sites. Where possible, we have compared our results to those of Henry Fitch (1960, 1970, 1999; Fitch and Shirer, 1971), whose mark-recapture research on this species in eastern Kansas is the most extensive to date. Ecological studies conducted on *A. contortrix* in southern Ohio (McDuffie, 1960) and Pennsylvania (Dunning, 2007; Johnson, 2005) also were consulted.

METHODS

Study Site

Topography.—The study site encompassed a 485 ha parcel of basalt trap-rock ridge ecosystem located 4.75 km NW of Meriden, Connecticut. A habitat map of the study site is presented in Fig. 1. Two prominent basalt ridges are present. Chauncey ridge is ≈ 914 m in length and is located in the south-central region of the study area. This ridge begins northward at a ravine that seasonally feeds Bradley Hubbard Reservoir and continues south along the eastern shore of the Reservoir, terminating at Chauncey Peak and having an elevation of ≈ 200 m above mean sea level (MSL).

Extensive exposed cliffs are present on the western aspect of Chauncey ridge where elevation abruptly drops ≈ 150 m to the shore of Bradley Hubbard Reservoir. Below these cliffs are numerous open talus fields ranging in size from one hectare to over ten hectares. The eastern aspect of Chauncey ridge slopes gently to a wetland at ≈ 120 m above MSL; this vertical change in elevation occurs over a horizontal distance of ≈ 600 m. An active limestone quarry has altered a significant portion of the ridge's eastern aspect.

The second and much longer ridge (3.2 km) is Lamentation Mountain, also characterized by exposed basalt cliffs, talus slopes, and extensive woodlands. Lamentation Mountain has a summit of ≈ 220 m above MSL with elevations along the ridgeline ranging from ≈ 80 m at the northern terminus to ≈ 170 m at the southern terminus. From the top of the Lamentation Mountain ridgeline the elevation drops dramatically on the western cliff side of the mountain. Like Chauncey ridge, the western aspect of Lamentation is characterized by steep, open talus fields. The eastern aspect at the northern terminus has a gentle decline in elevation from the summit, while elevation at the southern terminus drops abruptly to the western shore of Bradley Hubbard Reservoir.

Two primary hibernacula were located in this study. Hibernaculum 1 was used by 89% of study subjects and is located on the lower eastern slope of Lamentation Mountain. This hibernaculum consists of an extensive open talus field, rectangular in shape and approximately 0.8 ha in size. The other site (Hibernaculum 2) was used by 11% of study subjects and is located on the upper western slope of Chauncey Peak. It comprises a large open rectangular talus field approximately 0.4 ha in size.

Vegetation.—Lower elevation vegetation is primarily mixed deciduous forest. Ground cover consists almost exclusively of decomposing leaf litter. Mid-elevations contain extensive areas of hemlock (*Tsuga*) in addition to hardwoods, consisting mainly of oaks (*Quercus*), hickories (*Carya*), beech (*Fagus*), and maples (*Acer*). Many of the hemlock stands were dead or dying due to an ongoing woolly adelgid (*Adelges tsugae*) infestation,

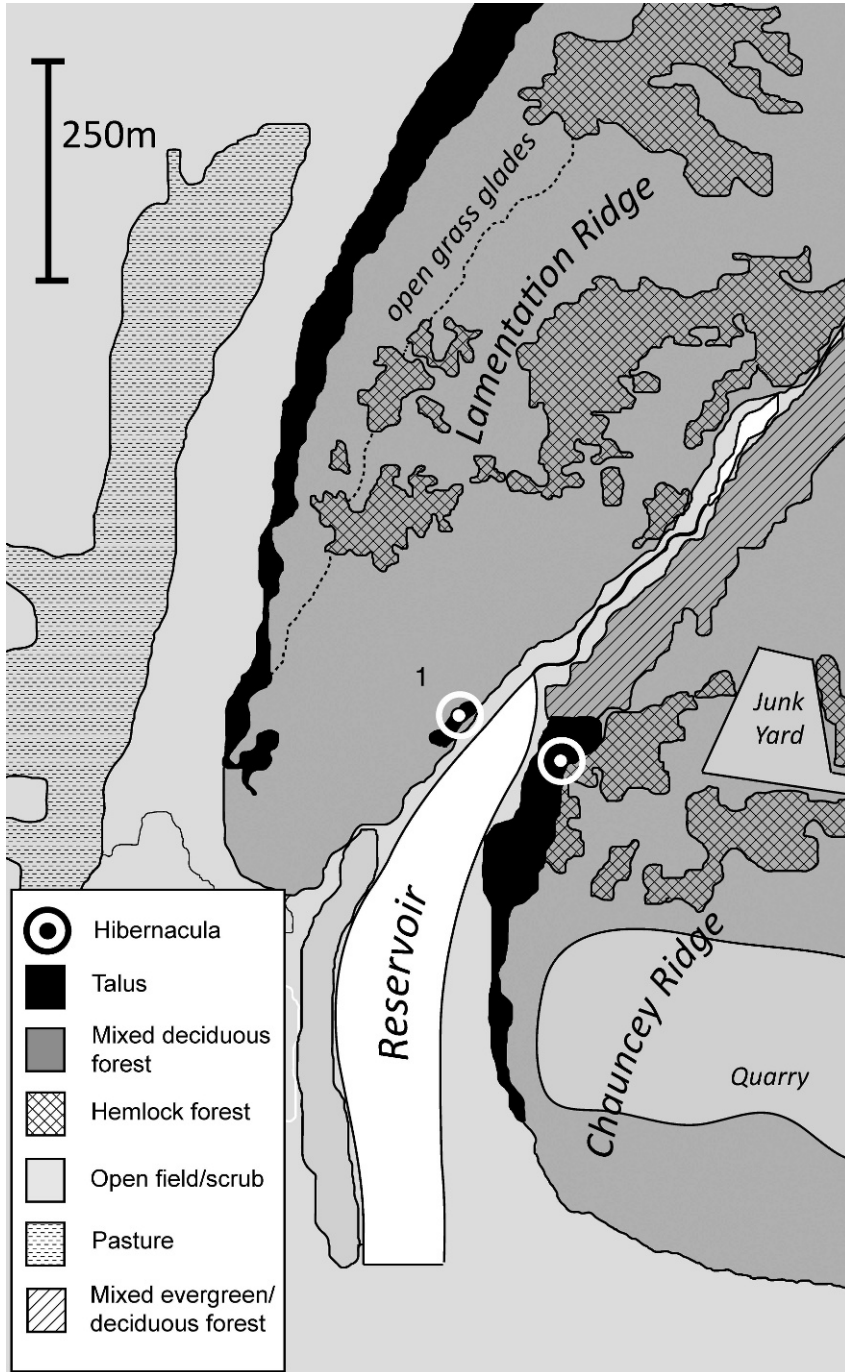


FIG. 1.—Characterization of major habitat types of the *Agkistrodon contortrix* study site. Location of Hibernacula 1 and 2 are designated by open circles.

and various hardwoods (e.g., maples and oaks) have penetrated these areas. Consequently, the character of the mid-elevation forest is more open with little or no vegetative ground cover. Upper ridge elevations are mixed deciduous although the forest is considerably more open, the ground cover being composed of large expanses of glade-like grasses and sedges (Fig. 1).

The western aspects of both ridges drop abruptly at exposed cliff faces often ≥ 50 m in height, below which are open talus fields. Vegetation along the margins of the talus fields is dominated by evergreens (*Pinus*), while vegetation within the fields is primarily Virginia Creeper (*Parthenocissus quinquefolia*) and Poison Ivy (*Toxicodendron radicans*).

Climate.—Climatic data (1960 to 1990) were obtained from the Meriden Markham Municipal Airport at Meriden, Connecticut ($41^{\circ} 30' 31.3730''\text{N}$; $072^{\circ} 49' 46.1220''\text{W}$; about 7.6 km from the study site). During the active season of *A. contortrix* (April through October), the mean monthly high and low temperatures for the 30-year period were 22.5 C and 11.2 C, respectively.

Mean monthly high and low temperatures during the time when snake activity is restricted to the vicinity of the hibernacula are 11.7 C and 1.4 C (March to April), and 19.4 C and 9.2 C (late September to October). Mean monthly high and low temperatures for the summer months combined (June through August) are 27.4 C to 15.6 C. Snowfall typically begins during late November when snakes are sequestered within hibernacula. Snow cover usually lasts through late March. During an average year, 34.1 cm of snowfall occurs during the 5–6 mo of winter. Rainfall patterns are typical for the northeast Atlantic seaboard states.

Field and Surgical Procedures

Adult subjects were initially located by intensive searching of the study site. During later months of the project new animals were added by locating them in close proximity to existing radio-marked animals. Following initial capture, snakes were transported to the laboratory (The University of Connecticut) where multiple body measurements were

made. Measurements for each snake included body mass (BM: ± 0.5 g using a triple beam balance), and snout–vent length and tail length (SVL: ± 0.2 cm; TL: ± 0.2 cm, using a non-stretchable cloth measuring tape while the snake was restrained in a clear acrylic tube). All individuals encountered at the study site were permanently marked for identification using intramuscularly injected passive integrated transponder (PIT) tags (125 kHz 12 mm Biomark, Boise, Idaho, USA). PIT tags were injected one-third of the body length anterior from the cloaca and the last three characters of the 10-character PIT tag code were used as an identification code for all records pertaining to an individual. Last, 0.1 ml of blood was collected from each animal for future DNA studies of parental assignment and kinship. DNA blood samples were stored under refrigeration in 100% ethanol.

During the three-year study, 35 adults (20 males, 15 females) were implanted with radio-transmitters (Holohil Systems Ltd., Carp, Ontario, Canada 5.5 gm SB-2T). However, subjects were periodically lost to predation or transmitter failure over the course of the study. In addition, because pregnant snakes frequently reduce their movement during gestation (Brown et al., 1982; Fitch, 1960; Reinert and Kodrich, 1982; Shine, 1979), females implanted early in the active season—(when pregnancy cannot be accurately established)—that later proved to be pregnant were not included in the analyses of activity range and movement. However, general movement trends of pregnant females are presented, and parturition dates recorded in the field ($n = 8$) and laboratory ($n = 17$), also are reported here. For the current study, complete spatial data were available for analysis from 10 adult males and 8 adult females. Spatial data for these 18 individuals, in addition to body sizes for all 35 adults, are given in Table 1.

Surgical implantation of the radio-transmitters followed published methods (Reinert, 1992). Transmitters were $<5\%$ of body mass. Surgery was performed within 24 h of capture, and each animal was held overnight and then released at the site of capture within 24 h post-surgery. Battery life expectancy for the

SB-2T model transmitter is 12 mo; therefore, transmitters were replaced annually with new units, with each animal undergoing two or three transmitter surgeries during the life of the study.

Radio-tracking Procedures

Subjects were located every two days on foot using a hand-held three-element folding Yagi antenna and a standard radio receiver (Model LA12-Q, AVM Instrument Co., Ltd., Colfax, California, USA) from late March until late October. Ingress to hibernation typically occurs in mid-October and from this time until egress in late March animals remained within the hibernacula. During the period of hibernation, animals were monitored once every week to assess transmitter function. Weather data (e.g., temperature, humidity, rainfall, wind speed) were collected daily during the active season in 2002 and 2003 and are presented in Fig. 2 and in Appendix I.

For each radio-tracked animal located, Universal Transverse Mercator (UTM) coordinates were recorded using a handheld GPS unit (Trimble GeoExplorer 3, Trimble Navigation Limited, Sunnyvale, California, USA). Coordinate positions were corrected using Trimble Pathfinder Office software (University of Rhode Island base station; 41° 29' 20.15818" N, 71° 31' 39.77858" W) and exported into ArcView 3.2 Spatial Analysis software (Environmental Systems Research Institute, Inc., Redlands, California, USA).

Data Analysis

Movement distances and activity range sizes were calculated using the Animal Movement Extension in ArcView 3.2 (see Hooge et al., 1999). Data were analyzed monthly (April through October), seasonally (reproductive vs. non-reproductive), and by year (2002, 2003). The variables were activity range size (hectares), total distance traveled (meters), and mean distance traveled (meters). Activity range size was estimated using 100% minimum convex polygon (MCP) and kernel 95% and 50% contour intervals as determined by ArcView. Because a single point lying outside the normal range of an animal can artificially inflate activity range size, range estimates

were recalculated after removing 5% and 10% of outliers using the Animal Movement harmonic mean outlier removal procedure. Comparisons of values prior to and following outlier removal showed no significant outlier effect; therefore, only values prior to outlier removal were used in the statistical analyses. For kernel estimates of activity range size, smoothing values were determined using least-squares cross-validation (Seaman et al., 1999).

Movement distances were calculated by using the distance function in the Animal Movement Extension in ArcView. Although straight-line estimates of movement can underestimate actual distance moved by as much as 50% (Madsen, 1984; Secor, 1992; Tiebout and Cary, 1987), the logistics of continuously monitoring a large number of individuals precluded direct measurement of all movements. Consequently, analysis of movements assumed that the underestimation was equal for both sexes, as has been demonstrated in one other temperate North American pitviper (Secor, 1994).

Statistical tests were performed using SAS Version 8.2 (SAS Institute, 1999. Cary, North Carolina, USA). Prior to performing analyses, all data were inspected for outliers, normality (skewness and kurtosis), and homogeneity of variance (Quinn and Keough, 2002; Zar, 1999). There were highly significant correlations among the three activity range parameters (MCP, 95% kernel, 50% kernel activity range; $r^2 > 0.63$, $P < 0.006$), and MCP was chosen for all statistical analyses (see Row and Blouin-Demers, 2006). MCP, 95%, and 50% activity range estimates are provided in Appendix II. Previous studies have demonstrated that body size (e.g., SVL and body mass) is not necessarily a good predictor of certain spatial parameters in snakes (e.g., Gregory et al., 1987; Secor, 1994; Slip and Shine, 1988). A preliminary analysis (ANOVA) showed that while initial body size (SVL) in *A. contortrix* ranged from 55.5 cm to 84.5 cm, body size had no effect on either monthly movement distances ($F_{1,16} = 2.683$, $P = 0.12$) or monthly activity range size ($F_{1,16} = 2.106$, $P = 0.17$). Accordingly, body size was not included to minimize the number of variables in the statistical model.

TABLE 1.—Summary data for 35 adult *Agkistrodon contortrix* included in the described study. Identification codes in bold-face type designate individuals used in the statistical analyses.

ID	Sex	Initial capture	SVL (cm)	Mass (gms)	Transmitter replaced	SVL (cm)	Mass (gms)	Transmitter replaced	SVL (cm)	Mass (gms)	Tracking period
263	♂	7/1/2001	56.1	128.3	4/6/2002	56.5	130.5	5/1/2003	60.4	160.6	7/1/2001–10/20/2003
E36	♂	7/2/2001	76.9	299.6	4/12/2002	77.2	331.3	4/19/2003	78.2	315.6	7/2/2001–10/20/2003
104	♂	7/4/2001	78.1	315.5	4/15/2002	78.4	291.5	5/1/2003	79.6	301.2	7/4/2001–10/20/2003
96C	♂	7/10/2001	74.2	246.8	4/10/2002	74.4	267	5/1/2003	75.4	291	7/10/2001–10/20/2003
KLC	♂	7/10/2001	67	201.4	4/10/2002	67.4	207.7	5/1/2003	69.8	171.6	7/10/2001–10/20/2003
71C	♂	8/6/2001	82.9	454.5	7/18/2002	82.7	480.1	5/1/2003	83.8	443.7	8/6/2001–10/20/2003
D54	♂	4/1/2002	60.5	160.3				5/1/2003	62.1	145.5	4/1/2002–10/20/2003
825	♂	4/1/2002	70.1	281				5/4/2003	71.9	264.2	4/1/2002–10/20/2003
06A	♂	4/5/2002	84.5	360.9				5/24/2003	84.7	329	4/5/2002–10/20/2003
15A	♂	4/7/2002	70	172.3				4/14/2003	76.7	298	4/7/2002–10/20/2003
A51	♂	9/17/2001	70	172.3	4/17/2002	69.9	166.3				9/17/2001–10/15/2002
618	♂	6/11/2001	88.5	373							
740	♂	8/24/2001	79.1	225.4							
14C	♂	9/24/2001	72.3	144.5							
4GH	♂	8/31/2002	77.3	347.5							
942	♂	4/29/2002	78.2	291.2							
106	♂	6/12/2001	68.2	176.9							
536	♂	5/22/2002	62.5	177.9							
RAB	♂	5/29/2001	72	253							
821	♂	7/5/2001	67.5	149.3							
B1F	♀	7/10/2001	57.5	183.9	5/17/2002	60.3	169.7	5/3/2003	60.4	191.7	7/10/2001–10/20/2003
C29	♀	8/31/2001	54	152	7/17/2002	55.5	156.3	5/1/2003	55.7	150.1	8/31/2001–10/20/2003
700	♀	9/5/2001	70.9	201.7	7/9/2002	71.7	221.3	5/1/2003	73.2	229.3	9/5/2001–10/20/2003
770	♀	9/28/2001	59.5	131.5	4/17/2002	60.2	144	5/1/2003	62.9	146.4	9/28/2001–10/20/2003
805	♀	4/1/2002	64.5	203.8				5/2/2003	65	192.4	4/1/2002–10/20/2003
E02	♀	4/3/2002	64.7	145.7				5/3/2003	66.4	165.8	4/3/2002–10/20/2003
E64	♀	4/7/2002	57	191.9				5/23/2003	59.4	203.1	4/7/2002–10/20/2003
62B	♀	4/18/2002	67.2	174.5				5/2/2003	68.1	160.9	4/18/2002–10/20/2003
155	♀	6/12/2001	88.5	529							
095	♀	6/12/2001	70.5	246.2							
850	♀	8/15/2001	61	158.3							
A0c	♀	7/14/2001	67.8	178.8							
E76	♀	6/29/2001	63.5	152							
95D	♀	6/20/2001	59.5	229.4							
53C	♀	6/10/2002	66.5	302.6							

AR = activity range size

TD = total annual distance moved

MMAR = mean monthly activity range size

MMD = mean monthly distance moved

The effects of sex, year, and season on activity range and movement parameters were determined using mixed, within-subjects repeated measures analyses of variance (PROC MIXED in SAS; see Wolfinger and Chang, 1995, for code details). Although data were collected from 2001–2003, the two most recent years for each individual were used in the statistical analyses as use of these years represented the most complete data set. Sex and season both were treated as between-subjects fixed factors, year as a fixed within-subjects repeated measure, and individual as a random factor. Measurements from the same animal (e.g., MCP, total distance traveled)

cannot be considered independent; thus, each parameter was analyzed separately and sequential Dunn-Sidak adjustments were applied to prevent compounding of Type I error ($\text{adj} = 1 - (1 - \alpha)^{1/k} = 0.017$ for most significant model with $k = 3$ parameters and the original α -level of significance set at $P < 0.05$). To achieve normality, MCP, total distance traveled, and mean distance traveled were natural-log, square root, and $y^{1/3}$ -transformed, respectively. Mixed-model statistical analyses require model fitting prior to examining the hypothesis tests, and Akaike (AIC) and Schwarz (BIC) information criteria were used to do so (Wolfinger and Chang, 1995).

TABLE 1.—Extended.

No. of Coordinates	Disposition	AR 2002 (ha)	AR 2003 (ha)	TD2002 (m)	TD2003 (m)	MMAR 2002 (ha)	MMAR 2003 (ha)	MMD 2002 (m)	MMD 2003 (m)
246	Released	37.69	40.69	6698.15	7292.84	5.7	7.28	861.18	859.16
245	Released	11.76	14.77	2103.18	3719.99	1.48	2.28	374.74	455.25
244	Released	14.43	12.54	4561.24	3634.26	3.08	2.95	906.17	716.31
240	Released	13.36	9.86	4920.43	3688.7	1.92	1.65	865.18	807.44
240	Released	8.67	8.19	2676.6	2751.2	1.03	0.97	481.41	511.14
237	Released	17.41	11.16	5159.64	3836.28	2.81	1.96	705.02	570.21
200	Released	9.29	13.41	4847.41	5593.15	1.62	2.27	582.18	745.71
201	Released	21.09	12.06	5795.35	3853.17	3.47	1.19	744.79	402.75
197	Released	35.81	44.49	5059.97	5813.87	4	7.41	746.23	711.09
196	Released	6.09	6.99	2085.75	2291.39	0.33	0.46	268.38	310.19
*	Transmitter failed winter 2002–2003	10.27	*	3053.67	*	1.22	*	436.24	*
*	Transmitter failed winter 2001–2002								
*	Transmitter failed winter 2001–2002								
*	Transmitter failed winter 2001–2002								
*	Transmitter failed winter 2002–2003								
*	Found transmitter 7/28/2002								
*	Found dead 5/15/2002								
*	Found dead 6/19/2002								
*	Moved onto private land								
*	Did not emerge from hibernation								
255	Released	4	5.3	800.1	970.3	0.13	0.19	839.58	901.44
234	Released	0.6	0.7	874.66	1056.33	0.11	0.14	114.29	195.79
222	Released	2.43	1.95	2418.52	1744.97	0.47	0.12	328.39	209.71
210	Released	1.44	0.93	1183.83	994.75	0.25	0.17	211.22	176.28
201	Released	9.9	8.05	3317.83	2477.64	1.33	1.01	495.55	313.42
200	Released	3.9	3.35	1891.43	1322.78	0.45	0.33	245.83	160.58
196	Released	3.45	4.61	2285.2	1637.55	0.53	0.65	276.33	304.94
191	Released	13.99	15.67	2751.8	3402.56	1.67	1.63	563.60	463.71
*	Found predated 8/12/2001								
*	Found predated 8/21/2001								
*	Transmitter failed winter 2001–2002								
*	Transmitter failed winter 2001–2002								
*	Pregnant; removed from study								
*	Pregnant; removed from study								
*	Pregnant; removed from study								

The compound symmetry covariance structure best fit all the data. When applicable, least squares means differences (LSMD) with Dunn-Sidak adjustments were used to interpret differences among levels of the main and interaction effects and to prevent compounding of Type I Error. Because the analyses of variance were unbalanced, Type III sum of squares were used to derive P -values.

Percent activity range overlap was used as an indicator of activity range fidelity and represented space used by an individual repeatedly in consecutive years. Overlap was determined by calculating the total area in hectares within the *union* of an individual's annual activity range for 2002 and 2003, the years for which the most complete data were

available. Subsequently, total (*union*) area was divided by the area within the *intersection* of the two annual activity ranges. Because the percent overlap of an activity range might be correlated with absolute range size (i.e., a greater probability that two large polygons will overlap compared to two small polygons within a fixed available area), an analysis was performed to examine the relationship between percent overlap and total range size. Results showed no relationship ($F_{1,16} = 0.002$, $P = 0.96$), which suggests that the observed overlap of annual activity ranges is a reasonably robust proxy for fidelity to particular areas. Subsequently, the effect of sex on activity range overlap was determined using analysis of variance with individuals as a

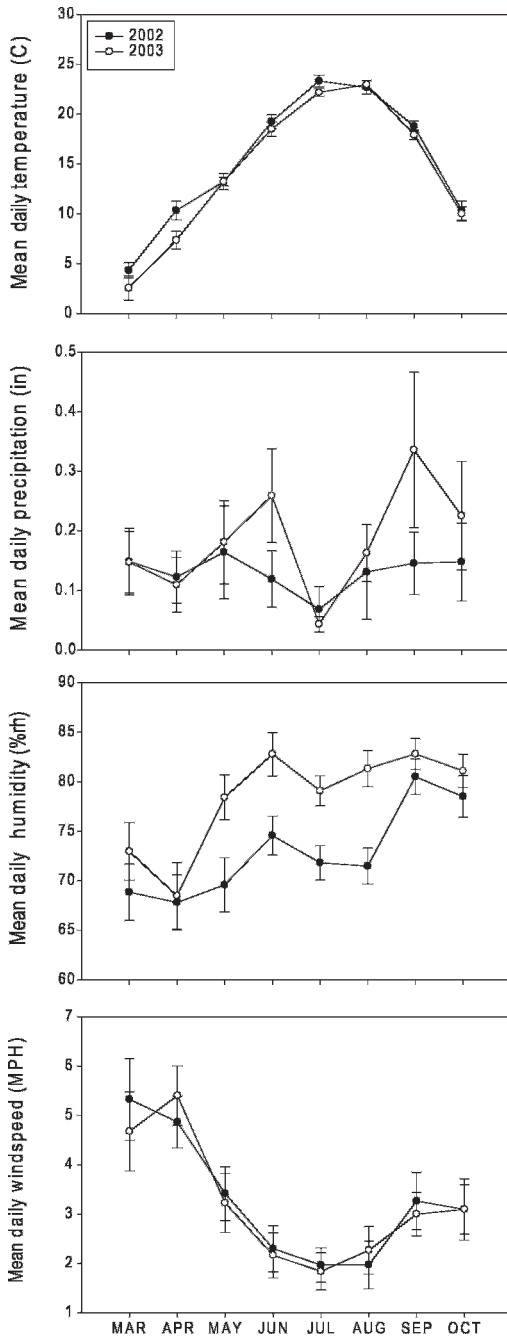


FIG. 2.—Climate data collected at the Meriden, CT study site for 2002 and 2003. Temperature, humidity and wind speed monthly means are presented as the mean of daily averages (mean of high and low). Precipitation is presented as monthly mean of daily total precipitation.

random factor. Repeated measures analyses of variance and linear regression analysis were used to examine individual fidelity to movement distances and activity range size for the years 2002 and 2003.

The method used to calculate individual fidelity to sites is illustrated in Fig. 3 (Smith, 2007). A circular buffer having a radius of 5 m was created in ArcView 3.2 surrounding each GPS point from two consecutive years. A single point, as well as any two or more points whose buffers overlapped, was designated a single site. The proportion of sites used in successive years was calculated by dividing the total number of sites used by an individual for those two years by the number of sites used in both years. The effect of sex on site fidelity was determined using analysis of variance.

Maximum straight-line distance moved from the hibernaculum was calculated for the years 2002 and 2003 by using the measurement tool in ArcView 3.2. The effects of sex and year on maximum straight-line distance were determined using mixed, within-subjects repeated measures analyses of variance. Sex was treated as between-subjects fixed factors, year as a fixed within-subjects repeated measure, and individuals as a random factor. In all cases, means are presented with ± 1 SE.

RESULTS

Research Subjects

In addition to the subjects with radio-transmitters and PIT tags, many individuals ($n = 117$) were implanted with PIT tags only. The marked population consisted of 52.2% adult males ($n = 60$) and 47.8% adult females ($n = 55$). Two marked animals were juveniles (<20 cm SVL) and were not sexed. Mean SVL for males was 75.5 ± 1.7 cm, and 66.3 ± 1.0 cm for females. Mean body mass for males was 210.2 ± 15.3 g, and 184.7 ± 10.3 g for females. Based on body size (e.g., SVL), the majority of individuals were scored as sexually mature when first marked (see Fitch, 1960). Body sizes of the radio-tracked individuals used in the statistical analyses did not differ significantly from the total marked population (males: SVL $t_{55} = 0.71$, $P = 0.48$, mass $t_{55} = -1.29$, $P = 0.2$; females: SVL $t_{53} = 1.70$, $P =$

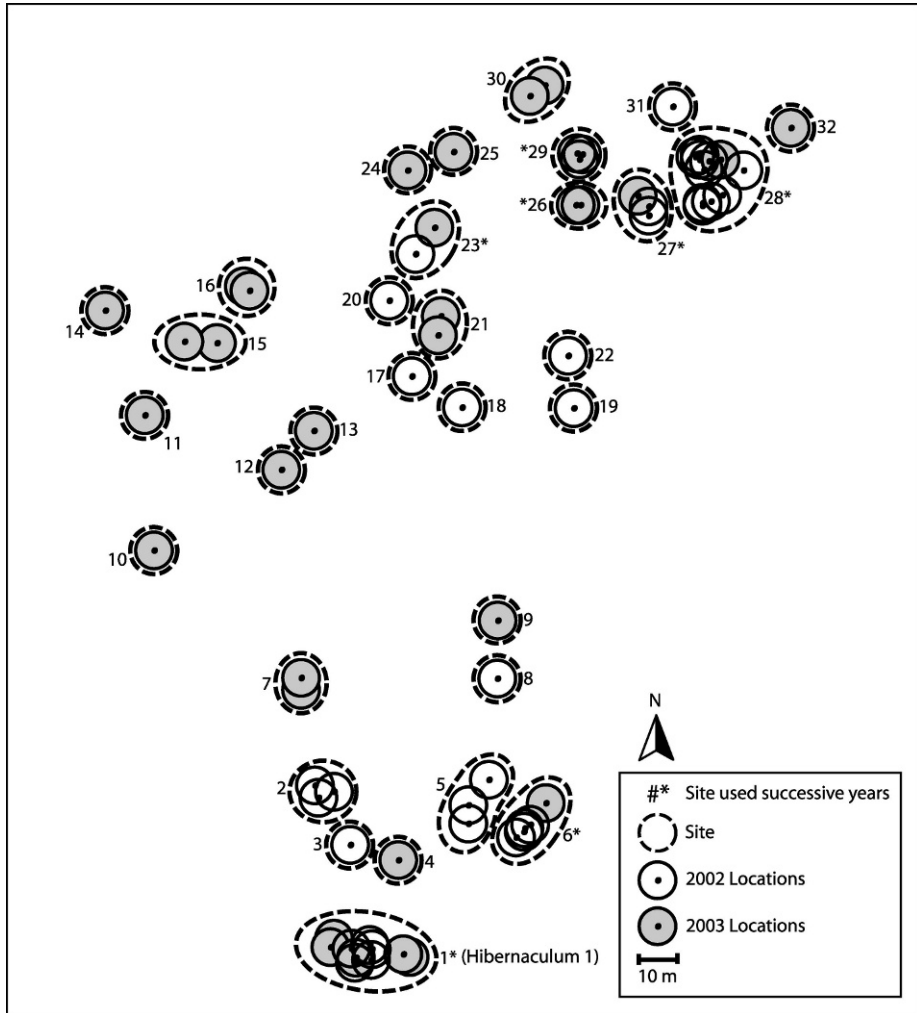


FIG. 3.—Method used to calculate individual fidelity to sites. A circular buffer (radius = 5 m) was created in ArcView surrounding each GPS point from two consecutive years. A single point, as well as any two or more points whose buffers overlapped was designated a single site. The proportion of sites used in successive years was calculated by dividing the total number of sites used by an individual for those two years by the number of sites used in both years. Hibernaculum location was not used in the calculation of site fidelity. In this example, six sites (6, 23, 26, 27, 28, 29) out of 31 sites were used in successive years (= 19.35%).

0.1, mass $t_{53} = 0.48$, $P = 0.63$). About 220 coordinates were recorded for each radio-tracked individual. The number of coordinates per individual did not differ significantly between males and females ($t_{16} = 1.03$, $P = 0.32$), and linear regression analysis showed no significant relationship between the number of coordinates used to estimate activity ranges and activity range size ($r = 0.06$, $P = 0.81$).

Activity Range and Movement Trends in Males

Individual males followed similar seasonal activity range and movement patterns. Males emerged from hibernation in late March and early April. The earliest observance of spring emergence was 17 March 2002. Following emergence, males remained near their hibernacula for ca. one month, basking during warm days (daily high temperatures > 15 C),

and retreating into the talus rock during cooler evenings (daily low temperatures $< \sim 4$ C). Movements during this period were limited (April: mean = 4.14 ± 1.69 m/day) and centered near the hibernacula, and activity ranges were small (April: mean = 0.37 ± 0.23 ha) compared to those attained by summer.

From May to early June, before moving to their summer feeding range, males migrated during daylight hours into a zone of transitional habitat located 100–200 m above the talus slopes (Fig. 1). Initiation of migration in Connecticut coincided with the elevation of nighttime temperatures above approximately 15 C. Transitional habitat consisted primarily of small areas of shaded talus, often only 10 m^2 in total size, surrounded by dense deciduous forest and having a canopy cover $> 50\%$ for vegetation less than two meters in height. Males increased (doubled) their movement distances in May (mean = 7.19 ± 1.77 m/day), but activity ranges remained small (May: mean = 0.35 ± 0.13 ha) compared to summer. This increase in male movement during May, with a concurrent absence of activity range expansion, is representative of males leaving hibernacula areas and moving into transitional habitat.

From mid- to late June, males moved from the transitional habitat into summer foraging ranges. Movement of males to foraging ranges regularly entailed migration distances of several hundred meters or more (Fig. 4). Once in summer ranges, males increased their activity range size (June: mean = 2.73 ± 1.08 ha) and initiated feeding. Movement distances also increased, both as a result of migration to summer ranges and movement within those ranges (June: mean = 20.76 ± 2.70 m/day).

Summer ranges for males were characterized by upper elevation open grassy glades, having sparse lower canopy cover ($< 50\%$ for vegetation two meters or less in height) and an upper canopy (> 5 m in height) of mixed deciduous forest hardwoods, mainly oaks (*Quercus*), hickories (*Carya*), beech (*Fagus*), and maples (*Acer*). Tracts of hemlock (*Tsuga*) ranging from 3–20 ha were interspersed within the deciduous forest (Fig. 1). Areas of dense hemlocks were seldom used by male

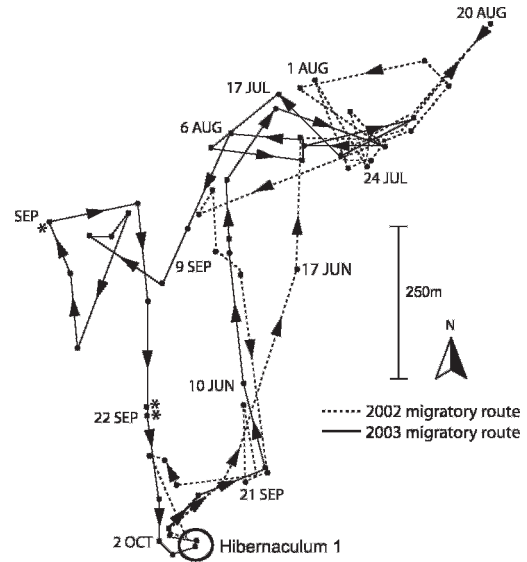


FIG. 4.—Seasonal movement pattern for *Agkistrodon contortrix* Male 06A in 2002 (dotted line) and 2003 (solid line). Asterisks (*) denote copulation events observed in the field for this individual. The hibernaculum is marked with bold circle.

Copperheads other than as corridors between more suitable habitat, most likely due to the lack of ground cover and low levels of available sunlight. Movement distances and activity range sizes for males increased only slightly during July (mean = 3.99 ± 1.04 ha; mean = 22.64 ± 2.91 m/day).

Males were almost exclusively nocturnal during July. Individuals located during daylight hours were found either in densely shaded areas, hollow tree trunks—either upright or fallen—or burrowed deeply within grass tussocks. Radio-tracking of animals in July alternated between days and evenings, and showed that the majority of movement occurred during the cooler evening hours (mean July high and low temperatures: 29 C, 17 C), typically beginning just after sunset.

In males, size of activity ranges and movement distances increased during August and September (August: mean = 6.49 ± 1.32 ha; 33.16 ± 3.90 m/day; September: mean = 5.90 ± 1.41 ha; 32.35 ± 4.57 m/day; (Figs. 5a–c). No shift in habitat accompanied the increase in activity range and movement in either month; rather, males simply expanded the boundaries of existing ranges.

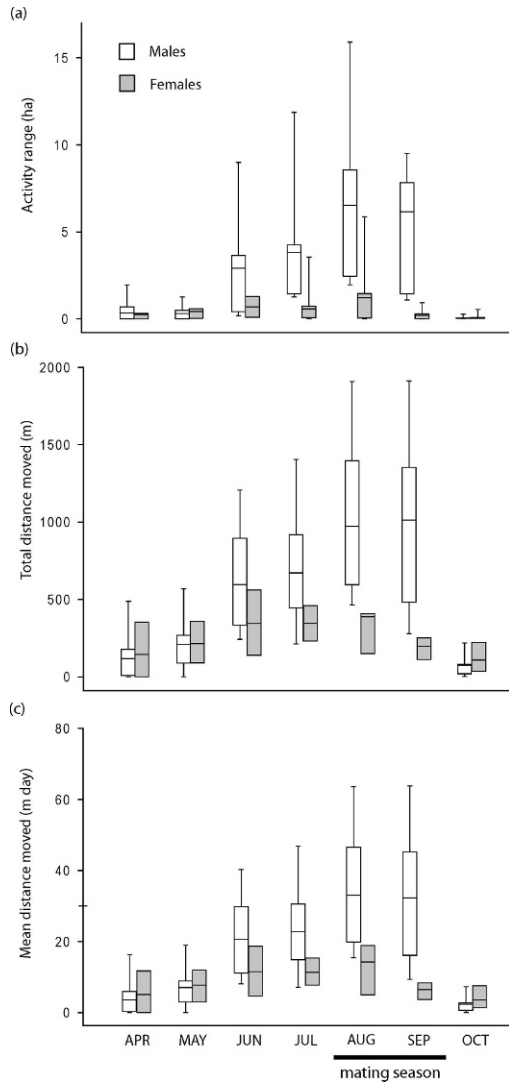


FIG. 5.—Box plots of monthly activity range size (a), total monthly distance moved (b), and mean monthly distance moved (c) of male and female *Agkistrodon contortrix* for 2002–2003 combined. The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the mean, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers above and below the box indicate the 90th and 10th percentiles.

During late September and early October, males initiated migration toward their respective hibernacula. As in emigration movements from hibernacula, migratory movements were typically straight-line and with few small-scale exploratory movements (Fig. 4). By mid-October,

all males had returned to the vicinity of their hibernacula. Male activity ranges in October were small (mean = 0.05 ± 0.02 ha) and were centered on hibernation sites, with the monthly movement recorded for this period (October: mean = 2.57 ± 0.58 m/day) representative more of migration from summer ranges than movement around hibernacula.

Activity Range and Movement Trends in Females

Females emerged from hibernation at the same time as males (late March and early April) and remained near the hibernacula until late April or early May. Basking occurred during warm days (daily high temperature $> \sim 15$ C). As with males, movements during this period were limited (mean = 5.24 ± 2.19 m/day). Female activity range sizes during April (mean = 0.32 ± 0.21 ha) were nearly identical to those for males. As for males, females were not observed to forage or feed during this period.

In May and early June, females initiated movements to zones of transitional habitat that was shared with males (Fig. 6). A brief description of this habitat is provided above. Movement distances and size of activity ranges were similar for both sexes (females: mean = 7.77 ± 2.12 m/day; mean = 0.46 ± 0.27 ha). Similar to males, female movement distances in May increased at a greater rate than did activity range size, reflecting migratory movement to transitional habitat.

Whereas males substantially increased their activity range size and distance moved in mid-June, females showed only a marginal increase in these spatial parameters (mean = 0.77 ± 0.31 ha; mean = 11.45 ± 2.58 m/day; Figs. 5a–c), but like males, females began to feed in mid-June. There was no difference between males and females in preferred summer habitat—both sexes used primarily upper-elevation grassy glades. Likewise, other than as corridors, females seldom used areas of dense hemlocks. Size of activity areas and movement distances for females decreased slightly during July (mean = 11.09 ± 2.28 m/day; mean = 0.67 ± 0.37 ha). Movements seemed to be related to episodes of foraging, and, like males, females were almost exclusively nocturnal during this period.

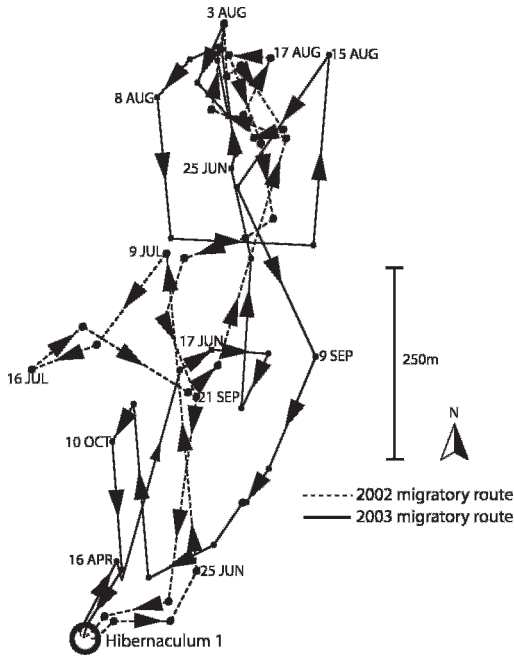


FIG. 6.—Seasonal movement pattern for *Agkistrodon contortrix* Female 62B in 2002 (dotted line) and 2003 (solid line). The hibernaculum is marked with bold circle.

As presented above, males showed a greater than 17-fold increase in activity range size and a five-fold increase in movement distance in August and September, as compared to April and May (Figs. 5a–c). In contrast, females did not show such large increases. Activity range sizes and movement distances for females were somewhat elevated in August (mean = 1.25 ± 0.60 ha; mean = 14.77 ± 4.03 m/day), although neither parameter was significantly different than that of other months during the active season (April to October). By September, activity range estimates and movement of females had returned to baseline levels recorded in April (mean = 0.26 ± 0.09 ha; mean = 6.42 ± 1.18 m/day).

By late September, females began migrating toward hibernacula (Fig. 6). Daily movements in October were restricted primarily to straight-line short distance migrations (mean = 3.65 ± 1.37 m/day) and were similar in extent to male migratory movements. Female activity ranges also decreased in size during October and became consolidated around hibernacula (October: mean = 0.09 ± 0.05 ha).

Spatial and Movement Parameters

Comparisons of annual activity range estimates (statistical analyses were conducted on monthly estimates only) indicated that male Copperheads maintain annual activity ranges that are larger than those of females (Figs. 7a & 8, Table 1). Annual activity range size for males during the two complete years (2002 and 2003) of the three-year study ranged from 6.09 to 44.49 ha (mean = 17.49 ± 2.68 ha). In contrast, annual female activity ranges for the same two-year period ranged from 0.60 to 15.67 ha (mean = 5.02 ± 1.15 ha).

Males showed greater annual movement than females (Fig. 7b, Table 1), and moved farther from hibernacula than did females ($F_{1,16} = 18.79$, $P < 0.01$; male mean = 769.5 ± 73.6 m; female mean = 363.1 ± 63.8 m). Annual total meters traveled for individual males during 2002 and 2003 ranged from 2085.75 m to 7292.84 m (mean = 4319.13 ± 337.70 m), while female annual total meters traveled ranged from 800.10 m to 3402.56 m (mean = 1820.64 ± 216.40 m). Although body size is not a reliable predictor of spatial parameters in this species, location of hibernacula was shown to influence movement distances ($F_{1,23} = 15.14$, $P < 0.01$) and activity range size ($F_{1,23} = 5.52$, $P = 0.045$). Hibernaculum 1 and its associated summer foraging/breeding habitat are separated by a greater straight-line distance than Hibernaculum 2 and its associated summer habitat, which might account for some of the observed variation among individuals (see *Habitat Associations*).

Males also exhibited significantly larger monthly activity range sizes ($F_{1,16} = 8.77$, $P = 0.0087$), greater monthly total distance traveled ($F_{1,16} = 19.02$, $P = 0.0004$), and greater monthly mean distance traveled than females ($F_{1,16} = 15.51$, $P = 0.0011$; Fig. 9a–c, Table 2). Considering males and females together, monthly activity range size ($F_{1,16} = 26.66$, $P = 0.0001$), monthly total distance traveled ($F_{1,16} = 39.44$, $P = 0.0001$), and monthly mean distance traveled ($F_{1,16} = 15.70$, $P = 0.001$) were greater in the mating season than in the non-mating season (Fig. 10a–c, Table 2). There was, however, a highly significant sex \times mating season interaction for all parameters analyzed.

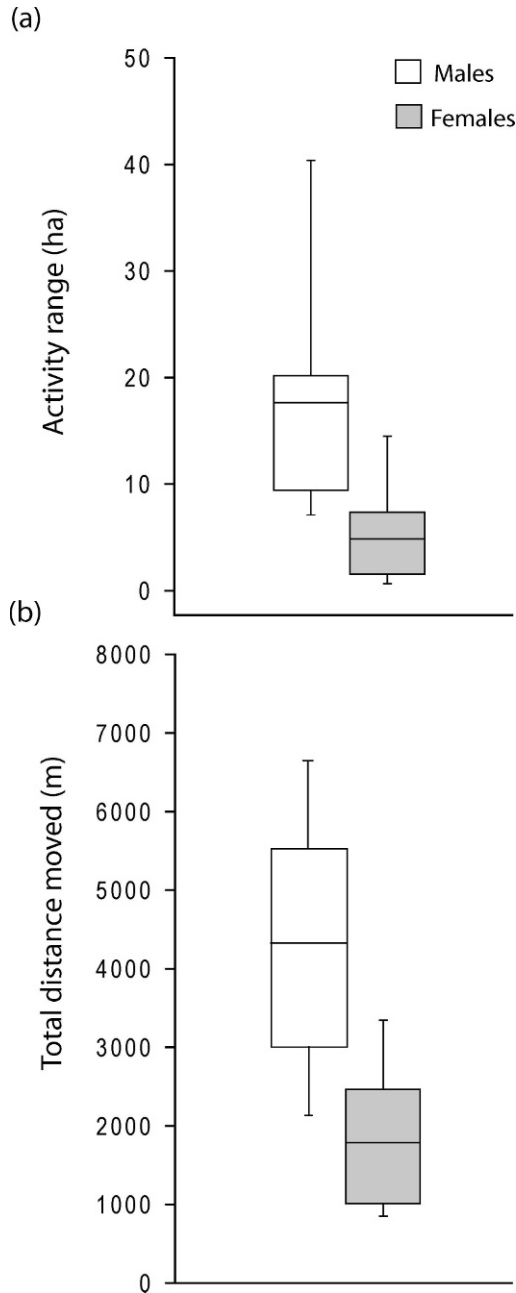


FIG. 7.—Box plot of annual activity range size (MCP; a) and annual total distance moved (b) of male and female *Agkistrodon contortrix* for 2002 and 2003 combined. Parameters of the box plots are provided in the Fig. 5 legend.

In all cases, monthly activity range size, monthly total distance traveled, and monthly mean distance traveled were significantly greater in males than in females during the mating season (August and September; LSMD with Dunn-Sidak adjustments; activity range, $t_{17} = 3.66$, $P = 0.012$; monthly total distance traveled, $t_{17} = 5.41$, $P = 0.0003$; monthly mean distance traveled, $t_{17} = 4.89$, $P = 0.0008$; Fig. 11a–c, Table 2). Furthermore, males exhibited significantly greater monthly activity range size, monthly total distance traveled, and monthly mean distance traveled in the mating season than the same males in the non-mating season (activity range, $t_{17} = 6.64$, $P < 0.0001$; monthly total distance traveled, $t_{17} = 8.81$, $P < 0.0001$; monthly mean distance traveled, $t_{17} = 6.63$, $P < 0.0001$; Fig. 11a–c, Table 2).

Monthly activity range size, monthly total distance traveled, and monthly mean distance traveled by males in the breeding season were significantly greater than shown by females in the non-breeding season (activity range, $t_{17} = 5.76$, $P = 0.0001$; monthly total distance traveled, $t_{17} = 7.59$, $P < 0.0001$; monthly mean distance traveled, $t_{17} = 5.81$, $P = 0.0001$; Fig. 11a–c, Table 2). No other comparisons (e.g., females in the mating versus non-mating season) approached significance.

Activity Range and Movement Trends in Pregnant Females

Pregnant females were not included in the analyses of activity range and movement; nonetheless, observations of their movements were recorded and estimates of female fecundity (litter size) were made. Groups of pregnant *A. contortrix*, ranging from 4–6 individuals, were commonly observed in July and August within the Connecticut study population. Pregnant individuals showed reduced movement and remained near the hibernaculum during gestation. For pregnant females carrying radio transmitters, mean monthly total distance traveled, monthly mean distance traveled, and monthly activity range sizes were not significantly different from zero.

Parturition in both the field and the laboratory took place exclusively from mid-to late summer (July–September), and all births recorded in the field occurred at or

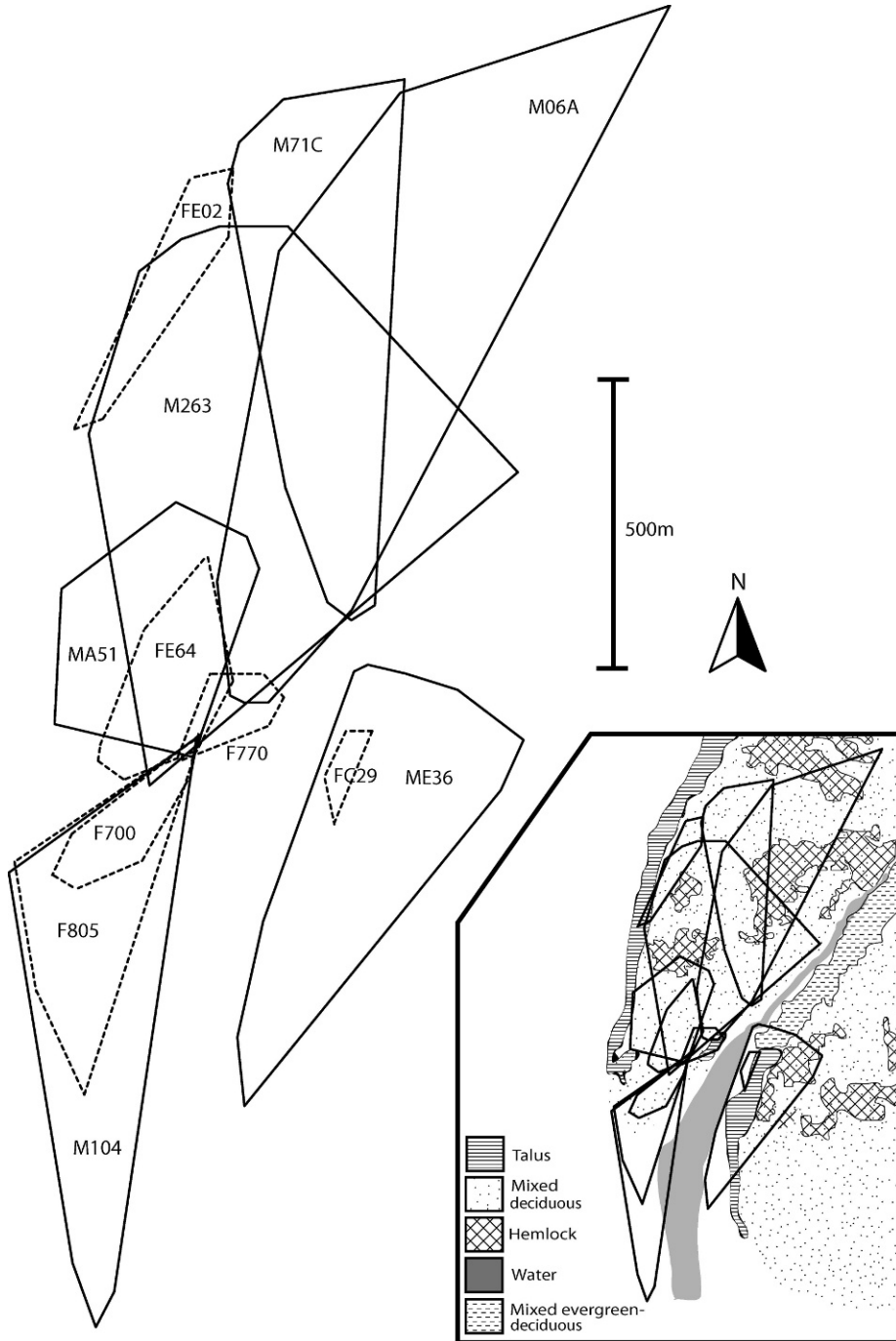
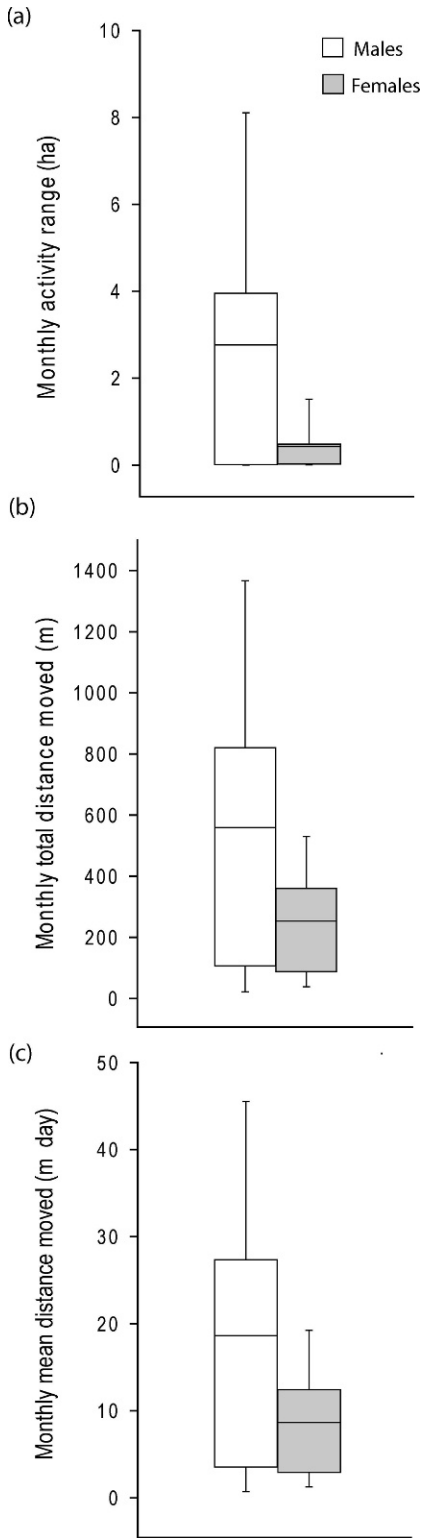


FIG. 8.—Comparison of annual activity ranges (MCP) for five male (solid line) and five female (dashed line) *Agkistrodon contortrix*. Inset shows location of home ranges in relation to major habitat types. Individuals depicted were selected using a random number generator and represent activity ranges for 2003.



close to the hibernaculum (den) associated with each female. Parturition was recorded eight times in the field during 2001–2003, with birthing dates ranging from 11 August to 13 September. Seventeen pregnant females were brought into the laboratory prior to parturition for a concurrent paternity study (range of days held in the laboratory prior to parturition = 7–79; mean = 58.7 ± 7.8 days). Birthing dates of females in the laboratory ranged from 29 July to 13 September (2001–2003).

Mating Season

Mating season was established by direct observations of courtship and copulation *in situ* and by levels of plasma testosterone in males (Smith et al., in press). Of the 42 copulations recorded in the field, 95.2% occurred during August and September (4.8% in July; 35.7% in August; 59.5% in September), concomitant with the expansion of activity ranges and increases in daily movements in males. Cloacal swabs taken from females in April, May, and June showed no evidence of recent copulation. Only two breeding events were observed in July (the evening of 29 July 2003 and the morning of 30 July 2003), representing the earliest observation of courtship and copulation. The distribution of activity range centroids (Jenness, J. 2006. Center of Mass, center_of_mass.avx extension for ArcView 3.x., Jenness Enterprises) for females in 2003 showed that they were dispersed during the mating season, in contrast to the months when mating was absent (Fig. 12).

Copulation was observed both during daylight and evening hours, although most movement in both sexes occurred in the evening. Males often courted two different females on consecutive days, with the movement between each female being 100 m or more. Also, it was common for the initial

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FIG. 9.—Box plots of monthly activity range size (MCP; a), monthly total distance moved (b), and monthly mean distance moved (c) of male and female *Agkistrodon contortrix* for 2002 and 2003 combined. Parameters of the box plots are provided in the Figure 5 legend.

TABLE 2.—Summary of the effects of sex, year, and breeding season on minimum convex polygon (MCP) and movement parameters in *Agkistrodon contortrix*; The breeding effect refers to the analysis of differences between months comprising the breeding (August, September) and non-breeding (April, May, June, July, October) seasons. Significant *P* values are in bold-face type.

Parameter	Effect	F	P	Interpretation
Home Range (MCP)	Sex	$F_{1,16} = 8.77$	0.0087	$\sigma > \varphi$
	Year	$F_{1,14} = 0.53$	0.4779	
	Breeding	$F_{1,16} = 26.66$	0.0001	Breeding > Non-breeding
	Sex*Year	$F_{1,14} = 1.35$	0.264	
	Sex*Breeding	$F_{1,16} = 7.76$	0.0127	$\sigma_{\text{breeding}} > \varphi_{\text{breeding}}$; $\sigma_{\text{breeding}} > \sigma_{\text{non-breeding}}$
	Year*Breeding	$F_{1,14} = 0.00$	0.9702	
Total meters traveled	Sex	$F_{1,16} = 19.02$	0.0004	$\sigma > \varphi$
	Year	$F_{1,14} = 0.016$	0.6931	
	Breeding	$F_{1,16} = 39.44$	0.0001	Breeding > Non-breeding
	Sex*Year	$F_{1,14} = 0.01$	0.9338	
	Sex*Breeding	$F_{1,16} = 17.40$	0.0006	$\sigma_{\text{breeding}} > \varphi_{\text{breeding}}$; $\sigma_{\text{breeding}} > \sigma_{\text{non-breeding}}$
	Year*Breeding	$F_{1,14} = 0.01$	0.907	
Monthly meters traveled	Sex	$F_{1,16} = 15.51$	0.0011	$\sigma > \varphi$
	Year	$F_{1,14} = 0.29$	0.6018	
	Breeding	$F_{1,16} = 15.70$	0.001	Breeding > Non-breeding
	Sex*Year	$F_{1,14} = 0.04$	0.8512	
	Sex*Breeding	$F_{1,16} = 15.47$	0.0011	$\sigma_{\text{breeding}} > \varphi_{\text{breeding}}$; $\sigma_{\text{breeding}} > \sigma_{\text{non-breeding}}$
	Year*Breeding	$F_{1,14} = 0.05$	0.83	

female to be in the presence of a new male within one to two days following the first copulation. Individual males often relocated and copulated with the same female over the course of a single season. As a result, the 42 copulations that were recorded represent matings between 21 males and 16 females.

Fidelity to Activity Range and Hibernacula

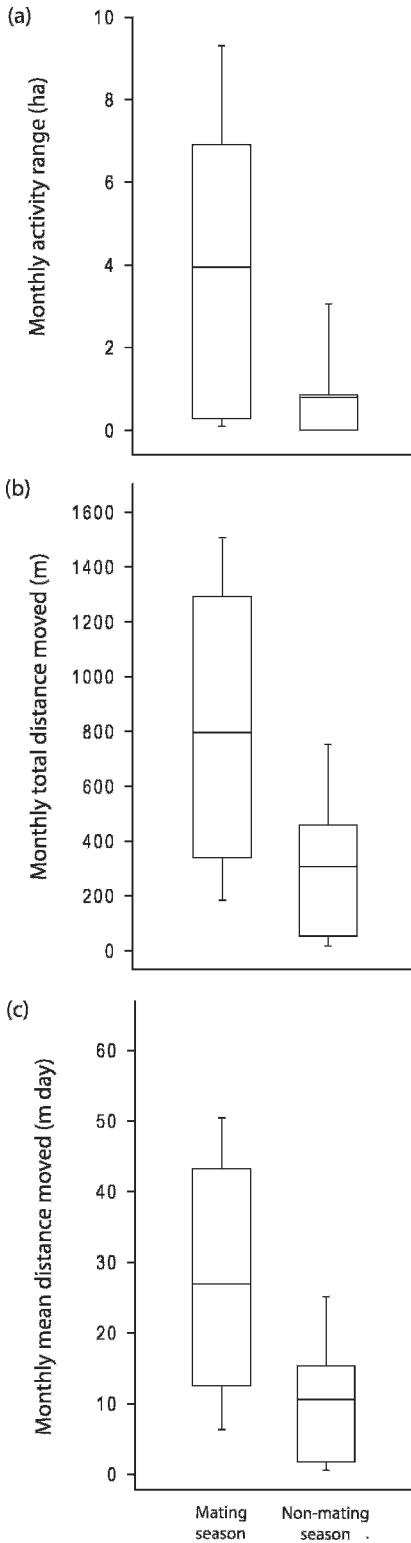
Both males and females showed high annual fidelity to activity range locations as well as high consistency in annual activity range size ($r^2 = 0.95$) and annual movement distances ($r^2 = 0.94$). However, there was a significant effect of sex on fidelity with males showing greater annual fidelity than females to activity range location ($F_{1,16} = 15.08$, $P = 0.001$). Percent overlap in annual activity range location among males ranged from 29.3% to 84.6% (mean = $61.7 \pm 0.1\%$). A single male had a percent overlap (29.3%) considerably less than other males in the study (this male was likely sexually immature during the initial year of the study) and when these data are not included, mean male percent annual activity range overlap increased to $67.1 \pm 0.1\%$. In two instances, males showed very

high levels of fidelity to annual activity range location, with nearly complete overlap between years (Fig. 13). In contrast, overlap of female annual activity ranges ranged from 29.8% to 55% (mean = $39.7 \pm 0.1\%$). Finally, females showed evidence of slightly higher annual fidelity to sites (female mean percentage of sites used in two successive years = $20 \pm 2\%$; male mean percentage of sites used in successive years = $14 \pm 0.2\%$) although this relationship was not statistically significant ($F_{1,16} = 1.21$, $P = 0.30$).

Fidelity to specific hibernacula was 100% in both males and females. Two hibernacula were investigated; one on the lower slope of Lamentation Mountain, and the other located on Chauncey Ridge (Fig. 1). Subjects using summer habitat on upper Chauncey Ridge always hibernated in the Chauncey Peak hibernaculum (Hibernaculum 2), whereas individuals using summer habitat on upper Lamentation Mountain always hibernated in the Lamentation Mountain hibernaculum (Hibernaculum 1).

DISCUSSION

The present radio-telemetric study provides a broad and detailed analysis of the daily



movements and activities of the Copperhead (*Agkistrodon contortrix*) at the northeastern extreme of its range (Campbell and Lamar, 2004; Gloyd and Conant, 1990). In many respects, our results are similar to those of previous studies of other populations of *A. contortrix*; however, we have been able to collect more details of individual activities (Fitch, 1960; Fitch and Shirer, 1971; McDuffie, 1960). For example, we show that sex differences in activity range and several movement parameters are pronounced. Furthermore, unlike populations of *A. contortrix* from more southern (e.g., Texas) or western (e.g., Kansas) regions where there are two pronounced mating seasons (late summer/early fall and spring) per annum (e.g., Aldridge and Duvall, 2002; Fitch, 1960; Fitch and Shirer, 1971; Schuett et al., 1997), the mating season of the present population was restricted to a single period (late July through September). This type of mating system, which lacks a mating season in spring, has been described for other North American pitvipers (Graham et al., 2008; Schuett, 1992; Schuett et al., 2005). Although further study is necessary, other populations of *A. contortrix* are suspected to show this type of mating season (e.g., McDuffie, 1960).

Activity Range and Movement Parameters

Sex differences in activity range size and movement parameters within our study population of *A. contortrix* are similar to those seen in several other pitviper species, such as the Cottonmouth (*A. piscivorus*) and the Timber Rattlesnake (*Crotalus horridus*; Reinert and Zappalorti, 1988; Roth, 2005). Adult male *A. contortrix* maintained activity ranges during the single mating season (late July through September) that were: (i) larger than those of adult females in both the mating

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FIG. 10.—Box plots of monthly activity range size (MCP; a), monthly total distance moved (b), and monthly mean distance moved (c) in male and female *Agkistrodon contortrix* combined. X-axis labels refers to months comprising the mating (August, September) and non-mating (April, May, June, July, October) seasons. Parameters of the box plots are provided in the Fig. 5 legend.

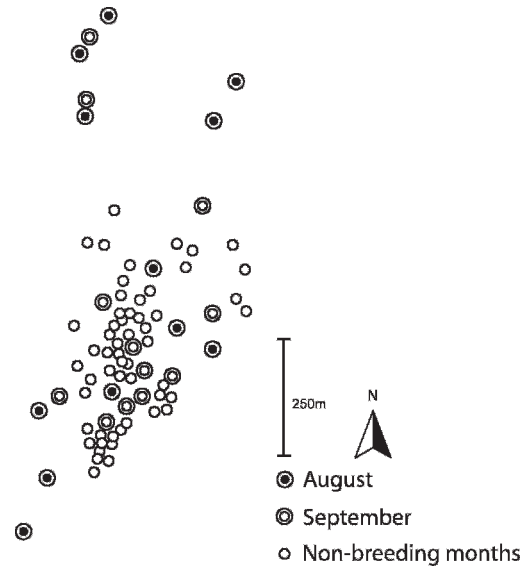
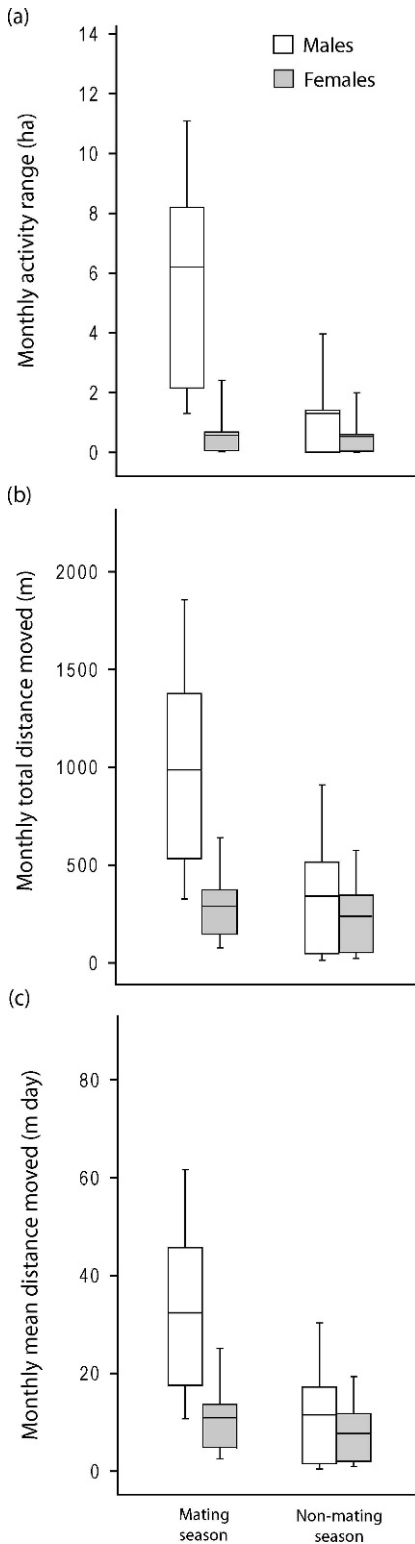


FIG. 12.—Distribution of activity range centroids for female *Agkistrodon contortrix* in 2003 for breeding months (August, September) and non-breeding months (April, May, June, July, October; Jenness, J. 2006. Center of Mass, center_of_mass.avx, extension for ArcView 3.x. Jenness Enterprises).

season and non-mating season, and (ii) larger than those of the same males during the non-mating season. Furthermore, movement distances of males showed similar trends relative to females, especially during the mating season. Based on results of other studies, it is likely that males made greater movements for the purpose of finding mates (e.g., Duvall et al., 1992, 1993; see Smith et al., 2008).

Fitch (1960) presented male and female *A. contortrix* activity range sizes (males: 9.87 ha; females: 3.44 ha) that differ from those presented here; nonetheless, the magnitude of difference between the sexes was roughly equivalent to our results (this study: males 3.5-fold greater than females; Fitch, 1960: males

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FIG. 11.—Representation of the sex \times breeding season interaction for monthly activity range size (MCP; a), monthly total distance traveled (b), and monthly mean distance traveled (c) of male and female *Agkistrodon contortrix*. Significant differences ($P < 0.05$) exist only between males in the breeding season and all other parameters. Parameters of the box plots are provided in the Fig. 5 legend.

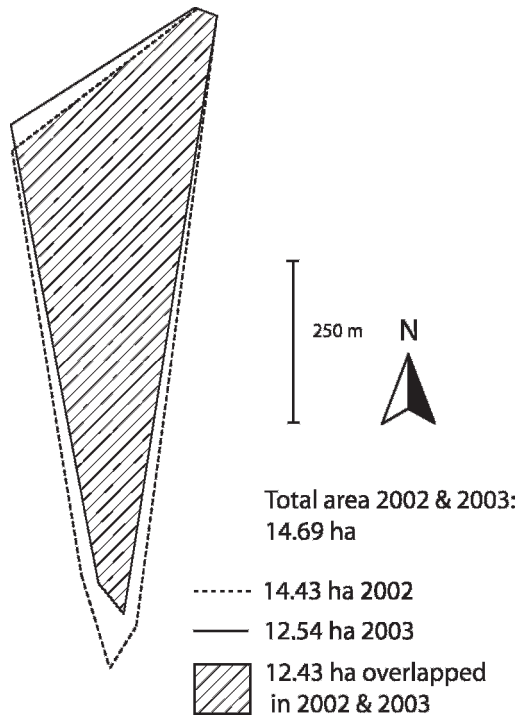


FIG. 13.—Home range fidelity in male *Agkistrodon contortrix* (ID 104). Of the total area used in 2002 and 2003 (14.69 ha) 84.6% (12.43 ha) was used in both years.

2.87-fold greater than females). However, the majority of work by Fitch (1960) on movements in a Kansas population of *A. contortrix* did not involve radio-telemetry (but see Fitch and Shirer, 1971), and activity ranges were estimates based on single point recaptures (Fitch, 1960).

Increases in male activity range size and movement distances during breeding periods in *A. contortrix* have been previously observed by both Fitch (1960) and McDuffie (1960). Our results, however, contrast with those of Dunning (2007), who showed that peak activity in Pennsylvania (estimated by number of encounters per month) occurred during June and July, rather than August and September. Because radio-telemetry was not used by Dunning (2007), it is likely that a trend toward nocturnal movement in mid- to late summer masked true activity levels of both male and females.

Although we favor the hypothesis that expansion of male activity ranges and increases in movements during the mating season

(late July through September) were directed to locating mates (e.g., Duvall et al., 1992, 1993; Smith et al., 2008), alternative explanations are possible. For example, increasing activity range size and movement distances might enhance opportunities for locating prey. An increase in activity range size and movements for both males and females in June coincided with the initiation of feeding, which was observed from mid-June through mid-October (Smith, in preparation). Observations of *in situ* feeding episodes suggests that males and females feed at similar rates on similar diets through the active season (Smith, 2007).

Other explanations for increased expansion of activity ranges and movements in males include predation pressure, environmental factors related to water balance, thermoregulation, and shelters. Although there is no evidence to suggest that any of these factors are causally related to changes in male movement, our data are not sufficient to rule them out at this time. However, because male *A. contortrix* adjusted the sizes of their activity ranges and movements at the onset of and throughout the single mating season, we contend that the most plausible explanation for the observed increases in activity range size and movement distances is that males are actively searching for females (Duvall et al., 1992, 1993; Kokko and Wong, 2007; Smith et al., 2008).

Spatial Ecology of Pregnant Females

Aggregations of four to six pregnant *A. contortrix* were observed in July and August within the Connecticut study population. Prior studies have also found aggregations of pregnant female Copperheads, sometimes in groups of 12 or more (Finneran, 1953; Fitch, 1960; Fitch and Clarke, 2002). Female aggregations have also been reported in other North American pitvipers (Brown et al., 1982; Graves and Duvall, 1993; Reinert and Kodrich, 1982; Wharton, 1966).

Pregnant individuals showed reduced movement during gestation as observed in other snake species (Brown et al., 1982; Keenlyne, 1972; Reinert and Kodrich, 1982; Shine, 1979; Viitanen, 1967) and often remained near the hibernaculum (Fitch, 1960; Keenlyne, 1972; McDuffie, 1960). Parturition in the field

occurred at or close to the hibernaculum associated with each female, and this phenomenon has been documented in other pitvipers and snakes (Brown et al., 1982; Graves and Duvall, 1995; Greene et al., 2002; Martin, 2002; Reinert and Kodrich, 1982; Shine, 1979; Viitanen, 1967). Indeed, female snakes frequently travel long distances to reach oviposition sites (Madsen, 1984; Parker and Brown, 1972), yet this is not typically the case in pregnant vipers.

Spatial Ecology and Fidelity

The observed fidelity to hibernacula was 100% by adults of both sexes, in agreement with the findings of Fitch (1960) and McDuffie (1960), although a direct level of fidelity was not calculated in either study. Migration between hibernacula was never observed and individuals exclusively used the separate summer ranges associated with each hibernaculum. The two dens (Lamentation Mountain and Chauncey Ridge), are separated by a straight-line distance of ≈ 200 m, including ≈ 112 m across Bradley Hubbard Reservoir, which likely represents a barrier to exchange between dens. Individuals were recorded moving more than 700 m in a period of two days and were regularly observed swimming within the Reservoir. Even so, males and females showed complete fidelity to dens—animals using summer habitat on upper Chauncey Ridge always hibernated in the Chauncey Peak den, while individuals using summer habitat on upper Lamentation Mountain always hibernated in the Lamentation Mountain den.

Although both males and females showed annual fidelity to the size of their activity ranges and movement distances, males showed significantly greater fidelity to activity range locations than females. Based on prior research that suggests (i) past reproductive success can influence site fidelity and activity range fidelity across taxa (Alcock, 1993; Greenwood, 1980; Greenwood and Harvey, 1982; Switzer, 1993, 1997; Wehner, 1981) and (ii) only males actively search for females (Duvall et al., 1992, 1993; King and Duvall, 1990), we predict strong selection on males to maintain similar activity locations between years. Location of food and shelter are

presumed to be the primary factors affecting the distribution of females. Given that female Copperheads are not the mate-seeking sex, they are not bound to a particular area for successful reproduction (Duvall et al., 1992; see Kokko and Wong, 2007). Conversely, males successful at locating and copulating with females during any given year are likely to use the same area in consecutive years.

In addition to fidelity to activity range location, and consistency in activity range size and movement distances, males and females also show strong fidelity to refuges sites located within their respective ranges (Brown and Duvall, 1993; Burger and Zappalorti, 1991; Ciofi and Chelazzi, 1994; Gerald et al., 2006; Reinert, 1993; Webb and Shine, 1997). Refuges, in the form of rock piles, hollow tree trunks, and hollow fallen logs, appear to be an important factor in shaping the routes used in navigating through ranges. Individuals returned repeatedly to the same refuges at approximately the same time each year. Refuges also appear important in annual migrations to and from hibernacula. Interestingly, we found evidence of slightly higher annual site fidelity in females, similarly alluded to by Webb and Shine (1997) in their study of *Hoplocephalus bungaroides*, although we did not find statistical significance in comparisons of site fidelity by males and females in the present study.

Although migration patterns are inherently difficult to ascertain in terms of fidelity, some generalizations can be made on the subjects in this study. Migration between seasonal ranges in many animals takes the form of a loop with little backtracking (e.g., Gregory et al., 1987; Macartney, 1985; Madsen, 1984; Sinclair, 1983) and this appears to be true for male and female Copperheads as well, although the paths taken from year-to-year are not identical. Movements leading away from the hibernaculum in late spring and returning to the hibernaculum in early fall are typically straight-line (see Duvall and Schuett, 1997), and it is not until individuals reach summer ranges that smaller “exploratory” movements are observed (Figs. 4 and 6). Thus, habitats between summer ranges and hibernacula appear to be used strictly as migratory corridors by *A. contortrix* (see Brown and Duvall, 1993).

Mating Season

Although populations of *A. contortrix* in more southern and western localities show two mating seasons per annum (Aldridge and Duvall, 2002; Fitch, 1960; Schuett, 1992; Schuett et al., 1996, 1997), we found only one in this study. In both southern and western populations, the first mating period occurs from late summer to early fall (Fitch, 1960; Schuett et al., 1997), followed by hibernation; the second mating season occurs in spring during the time individuals emerge from hibernacula. Courtship and copulation often occur at (or near) the hibernaculum (Fitch, 1960). In these cases, ovulation and fertilization occur in spring following the second mating season (Fitch, 1960). In our Connecticut population, individuals of *A. contortrix* did not show a post-hibernation (= spring) mating season, even though emergence from hibernation roughly corresponded to mid-April emergence (males and females) reported for Kansas (6–25 April: Fitch, 1960) and Ohio (mid-April: McDuffie, 1960). Consequently, in our study, only a single mating season (i.e., late July through September) was observed, and during this period males had expanded activity ranges and increased various movement parameters. A similar pattern consisting of a single late summer mating season was recorded from a population located in Shawnee State Forest in southern Ohio (McDuffie, 1960). This pattern may be more common than previously thought, not only in other populations of Copperheads (see McDuffie, 1960), but in its congener *A. piscivorus* (Graham et al., 2008; Hill and Beaupre, 2008; Zaidan et al., 2003) and other species of pitvipers (Aldridge and Duvall, 2002; Schuett, 1992; Schuett et al., 2002).

Although we favor the hypothesis that cold temperatures have a proximate causal role in shaping the reproductive activities of *A. contortrix* in our population (see Zaidan et al., 2003), it is premature to conclude that this is the exclusive environmental factor. Arguably, one of the most compelling reasons against the temperature hypothesis is that other, sympatric snake taxa, such as the natricine *Thamnophis sirtalis* and the colubrine *Coluber constrictor*, show a spring

mating season (Smith, C. F. unpubl. observations). Other populations of *T. sirtalis* from extreme regions (i.e., high latitudes) also mate in the spring (Aleksiuk and Gregory, 1974; Shine et al., 2001). Other proximate factors, therefore, are likely to have a role, though these remain unexplored. It also remains to be determined whether the mating season we describe is a stable feature of our study population rather than a facultative and transient response to seasonal temperature, or some other environmental factor (Schuett et al., 2002). Furthermore, historical variables related to phylogenetic history also need to be considered as potentially influencing mating seasons (see Schuett et al., 2002). For example, Douglas et al. (2009) present several lines of evidence suggesting that the eastern and western populations of *A. contortrix* are genetically divergent enough to be considered separate species.

Contrary to what might be expected, the greatest number of copulations ($n = 25$ in September) in this study did not occur when activity ranges and movement distances of males were at peak levels (August). However, it is reasonable to surmise that the August peak is a result of males actively searching for females. Once males locate females, they are likely to restrict their movements around patches of available females in September. Therefore, the size of activity ranges and movement distances begin to decrease in September. Not only are females widely dispersed during the breeding season, but based on the high percentage of pregnant females observed in the population (45%), reproductively available females are likely to be a scarce resource for searching males (Duvall et al., 1992). Thus, we suggest a male-biased operational sex ratio (Duvall et al., 1992, 1993; Emlen and Oring, 1977) in the present population. Under this condition, males of *A. contortrix* are expected to compete for access to females through scramble competition and/or fights (Duvall et al., 1992, 1993; Schuett, 1997). Although agonistic interactions between male *A. contortrix* occur in the laboratory (Schuett, 1997; Schuett et al., 1996) and have been observed in the wild (e.g., Fitch, 1960; Gloyd, 1947; Mitchell, 1981), no instances of male–male fighting

were observed in this study. It is more likely that males are competing primarily by way of prolonged scramble competition for priority-of-access to females (Duvall and Schuett, 1997; Smith et al., 2008), and male fighting is thus infrequent or rare. Certainly, further work is needed to address these questions.

Habitat Associations

Based on a preliminary analysis of vegetation abundance (Smith, 2007), foraging and breeding habitat was more broadly present on Lamentation Mountain (73 ha) than on Chauncey Peak (16 ha). Furthermore, for subjects associated with Lamentation Mountain, a straight-line migration of approximately 700 m was required to reach the centroid of available summer habitat, whereas a migration distance of about 150 m was required for individuals associated with Chauncey Peak. As a result, the size of activity ranges and movement distances were smaller for individuals that hibernated on Chauncey Peak. Thus, some of the variation within male and female annual activity range and movement estimates can be attributed to the distance needed to reach each respective summer range (Fitch, 1999).

Seasonal habitat use in *A. contortrix* in the present population roughly mirrored findings of previous studies (Fitch, 1960; Johnson, 2005; Reinert, 1984a). Males and non-pregnant females showed a preference for open canopy rocky habitats, talus slopes, and adjacent deciduous forest. Individuals also showed a preference for substrates consisting of leaf litter from deciduous trees (Fitch, 1960) and sustained use of open grassy habitat where available (Fitch, 1960), especially during summer months. While Johnson (2005) found a preference among females for rocky substrates regardless of sexual condition, and additionally suggested that non-pregnant females may prefer rocky substrates more so than males, we observed no such preference in our study. A similar preference was observed by Reinert (1984b) in *Crotalus horridus* and may be related to thermal requirements of follicular development in non-pregnant years.

Acknowledgments.—The authors gratefully acknowledge J. Victoria and L. Fortin, Connecticut Department

of Environmental Protection Wildlife Division, for permits, telemetry equipment, and funds to purchase radio transmitters and PIT tag supplies. Thanks also to S. Berube, H. Gruner, R. Gibson, and D. Hardy, Sr. Funding was provided by the American Wildlife Research Foundation, The University of Connecticut Department of Ecology and Evolutionary Biology Wetzel Fund, the Connecticut Department of Environmental Protection Non-game Fund, Sigma Xi, and a NSF Predoctoral Fellowship to CFS. The study was conducted under the supervision of The University of Connecticut Institutional Animal Care and Use Committee, protocol number S211 1201. We dedicate this paper to the memory of the late Dr. Henry S. Fitch.

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APPENDIX I

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Mean	
March 2002	0	1	10	-1	-3	4	7	7	12	6	0	2	2	10	7	8	2	1	3	2	5	-4	1	4	4	3	7	6	6	13	11	4	
Mean Temp C																																	
Mean Humidity	64	76	90	46	46	59	67	84	88	58	43	76	89	71	89	82	55	86	83	84	69	48	41	50	53	86	83	57	71	77	63	69	
Mean Wind	0	2	11	11	2	2	2	0	17	7	1	1	3	1	4	8	4	2	3	11	16	6	4	9	8	3	10	3	10	2	5		
Speed MPH																																	
Precipitation (in)	0	0.2	1.4	0	0	0	0	0	0.1	0.2	0	0	0.1	0	0	0.1	0.4	0	0.6	0	0	0	0	0	0.9	0.6	0	0	0.1	0.2	0.15		
April 2002																																	
Mean Temp C	11	6	11	4	1	2	2	8	14	13	9	7	17	19	20	22	24	25	19	15	11	7	5	6	7	4	7	8	6	8	11		
Mean Humidity	77	56	83	55	52	45	40	66	76	63	54	86	85	68	83	65	64	51	70	74	38	82	63	55	85	82	55	93	85	83	68		
Mean Wind	4	4	11	5	3	6	6	7	6	7	3	1	5	7	8	0	0	5	3	3	7	5	10	2	6	2	4	0	7	9	5		
Speed MPH																																	
Precipitation (in)	0.2	0	0.3	0	0	0	0	0	0	0.1	0	0	0	0	0.5	0	0	0	0.1	0	0.4	0	0	0	0.5	0	0	1	0	0.5	0.12		
May 2002																																	
Mean Temp C	8	8	11	10	13	14	18	16	11	18	13	11	8	11	11	14	19	8	7	6	7	10	13	17	15	14	19	18	20	20	22	13	
Mean Humidity	70	92	64	51	57	69	71	57	80	71	43	86	96	77	54	60	61	88	59	55	60	51	53	62	52	82	87	92	89	84	84	70	
Mean Wind	0	1	6	6	0	3	4	8	1	3	4	0	3	8	11	2	8	4	5	3	2	1	1	1	10	5	0	1	0	0	5	3	
Speed MPH																																	
Precipitation (in)	0	0.3	0	0	0	0	0	0	0	0	0	0	0.42	0.2	0	0	0	1.4	0	0	0	0	0	0	0	0	0	0.3	0	0	0.4	0.16	
June 2002																																	
Mean Temp C	21	18	16	14	21	18	13	13	17	19	22	19	14	14	13	17	18	18	19	19	19	22	24	24	21	26	26	24	24	23	19		
Mean Humidity	74	61	51	57	78	65	70	67	78	63	79	88	83	89	98	86	76	66	77	82	75	76	75	69	61	82	88	85	65	73	75		
Mean Wind	3	4	7	0	8	5	7	0	1	2	3	0	6	1	7	0	0	1	0	0	1	0	1	0	1	3	1	4	3	0	2		
Speed MPH																																	
Precipitation (in)	0	0	0	0	0.3	1	0.8	0	0	0	0	0.1	0	0.4	0.1	0.7	0	0	0	0	0	0	0	0	0	0.1	0.2	0	0	0	0.12		
July 2002																																	
Mean Temp C	26	27	29	28	23	22	21	23	26	23	18	18	20	22	24	23	21	27	26	23	23	24	27	21	18	18	19	21	28	28	26	23	
Mean Humidity	69	79	84	70	53	59	69	65	82	69	53	64	69	70	75	59	67	65	83	82	76	75	84	74	66	74	85	93	80	71	62	72	
Mean Wind	4	4	2	0	7	2	2	2	0	2	4	0	0	0	1	3	0	0	2	2	6	3	4	4	0	0	1	0	2	0	4	2	
Speed MPH																																	
Precipitation (in)	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0.6	0	0	0	1	0	0	0	0	0	0	0	0	0.07	
August 2002																																	
Mean Temp C	27	27	26	25	27	20	19	19	19	22	24	26	27	28	26	28	27	28	27	22	20	20	21	17	21	20	21	20	16	18	18	23	
Mean Humidity	64	82	76	73	86	53	61	66	63	64	67	62	76	72	77	81	75	73	50	81	66	74	75	83	75	71	58	56	89	86	81	71	
Mean Wind	0	0	0	0	1	7	5	0	1	0	0	0	0	0	3	7	0	0	5	2	1	0	5	0	5	0	0	6	5	8	0	2	
Speed MPH																																	
Precipitation (in)	0	1.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0.2	0	0	0	0	2.2	0.1	0	0.13	

APPENDIX I
Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Mean	
July 2003																																	
Mean Temp C	20	21	19	24	27	27	23	26	19	19	20	22	21	21	21	21	21	21	22	20	21	24	23	24	23	22	22	26	24	22	21	21	22
Mean Humidity	61	67	82	84	78	77	84	87	88	80	85	80	78	83	80	93	66	83	81	66	89	86	95	84	79	78	70	64	71	81	72	79	
Mean Wind	3	0	3	0	2	0	0	0	0	0	4	0	0	0	0	3	6	0	2	0	3	6	4	6	4	0	4	4	2	1	0	2	
Speed MPH																																	
Precipitation (in)	0	0	0	0	0	0	0	0.1	0	0.2	0	0	0	0	0	0	0.1	0	0.4	0.1	0	0.1	0.1	0.1	0	0	0	0	0	0	0	0	0.04
August 2003																																	
Mean Temp C	21	23	26	26	24	24	24	22	24	24	24	26	26	26	24	24	22	22	22	23	24	26	22	18	21	21	23	19	19	23	17	23	
Mean Humidity	93	92	87	93	87	87	90	97	91	89	87	84	86	81	77	81	85	82	77	79	81	81	54	55	71	77	78	65	82	83	69	81	
Mean Wind	2	3	0	6	7	2	0	3	3	6	6	4	1	0	0	0	0	3	0	0	0	0	8	6	0	0	0	0	2	6	5	2	
Speed MPH																																	
Precipitation (in)	0.2	0.3	0	0.8	0.4	0	0.3	0.6	0	0.3	0.4	0	0	0	0	0	0.9	0.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.16
September 2003																																	
Mean Temp C	17	15	17	20	20	18	18	19	17	16	19	18	17	23	23	19	17	18	22	22	18	17	18	15	17	17	20	18	14	11		18	
Mean Humidity	90	97	85	99	76	75	77	79	77	75	76	75	61	93	88	87	77	67	91	84	76	87	86	86	82	86	91	89	88	84		83	
Mean Wind	0	6	3	2	2	4	0	2	1	0	0	1	6	2	1	5	3	3	9	5	2	0	8	3	2	3	4	7	3	3		3	
Speed MPH																																	
Precipitation (in)	0.8	1.9	0	0.1	0	0	0	0	0	0	0	0	0.1	0.7	0.1	0.9	0	0	0.7	0	0	0	1.4	0	0	0	0	3.2	0	0	0	0.34	
October 2003																																	
Mean Temp C	10	11	7	9	9	7	8	13	17	12	16	13	14	11	14	10	8	7	3	6	15	7	3	3	4	14	16	10	14	9	11	10	
Mean Humidity	87	80	71	83	73	82	79	88	86	100	73	87	74	82	72	66	81	86	95	85	82	78	67	66	74	95	97	80	91	68	86	81	
Mean Wind	0	0	5	0	3	2	0	0	1	0	0	7	2	0	12	4	0	2	0	0	8	7	10	4	2	1	10	4	5	4	3	3	
Speed MPH																																	
Precipitation (in)	0	0	0	0	0	0	0	0	0	0	0	0	1.90	0	1.1	0	0.1	0.1	0.3	0	0.3	0	0	0	0	0.2	1.3	0.1	1.6	0	0	0.23	

APPENDIX II

Yearly home range estimates presented in hectares (minimum convex polygon [MCP] and 95% and 50% kernel) for *Agkistrodon contortrix* obtained using Animal Movement extension in ArcView 3.2 (ESRI) GIS software.

Animal ID	Sex	Year	Home range (MCP)	Home Range (kernel) 95%	Home Range (kernel) 50%
263	♂	2002	37.69	34.93	6.97
263	♂	2003	40.69	32.38	5.59
E36	♂	2002	11.76	1.52	0.23
E36	♂	2003	14.77	5.65	0.85
104	♂	2002	14.43	32.39	4.1
104	♂	2003	12.54	25.5	3.46
96C	♂	2002	13.36	35.51	8.91
96C	♂	2003	9.86	51.4	13.57
KLC	♂	2002	8.67	32.7	5.93
KLC	♂	2003	8.19	31.31	5.38
71C	♂	2002	17.41	28.36	3.51
71C	♂	2003	11.16	24.48	4.22
D54	♂	2002	9.29	7.91	0.87
D54	♂	2003	13.41	12.4	1.88
825	♂	2002	21.09	31.39	2.66
825	♂	2003	12.06	20.33	1.98
06A	♂	2002	35.81	55.35	9.62
06A	♂	2003	44.49	68.99	9.67
15A	♂	2002	6.09	7.17	1.35
15A	♂	2003	6.99	9.97	2.04
A51	♂	2002	10.27	19.29	2.76
B1F	♀	2002	4.0	8.26	1.23
B1F	♀	2003	5.3	3.35	0.93
C29	♀	2002	0.6	0.95	0.14
C29	♀	2003	0.7	1.34	0.24
700	♀	2002	2.43	4.23	1.15
700	♀	2003	1.95	2.94	0.31
770	♀	2002	1.44	2.11	0.4
770	♀	2003	0.93	1.59	0.29
805	♀	2002	9.9	7.68	1.22
805	♀	2003	8.05	6.95	1.03
E02	♀	2002	3.9	6.91	1.05
E02	♀	2003	3.35	7.95	1.27
E64	♀	2002	3.45	5.34	0.86
E64	♀	2003	4.61	4.07	0.51
62B	♀	2002	13.99	30.39	5.53
62B	♀	2003	15.67	21.94	1.86