

Further Notes on Growth of Juvenile Timber Rattlesnakes in Northeastern Kansas

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Introduction

Since April 2003, we have studied a small population of Timber Rattlesnakes (*Crotalus horridus*, Fig. 1) resident at the field station of The University of Kansas Environmental Reserves, considerably expanding on knowledge of the species summarized in Fitch (1999). Our earlier papers involved few recaptures of Timber Rattlesnakes marked by HSF from 1990–2002, although one notable recapture was of an adult male (Fig. 2) marked by HSF in 1978 (Fitch and Pisani 2002). Although eastern Kansas is the western limit of the distribution of *Crotalus horridus*, based upon life history parameters for this population (Fitch and Pisani 2006, Pisani and Fitch 2006), the species in northeastern Kansas does not appear to be at an area of climatic limitation as reviewed by Martin (2002). The area is a mosaic of wooded limestone ledges and open fields of mixed forbs

and grasses, with an abundant potential prey base of small rodents (Fitch and Pisani 2006, Pisani and Fitch 2006).

Fitch and Pisani (2006) documented the expected high correlation between rattle base-segment width and snout-to-vent length (SVL) of Timber Rattlesnakes in this population. In their Figure-1, they presented a population growth curve, in part utilizing data from incomplete rattles placed by employing a modification of Klauber's (1956) "tree ring" approach; pros and cons of the methodology were briefly discussed by Fitch (2002). Use of a capture-processing protocol that attempts to minimize stress to the snakes has resulted in a considerable number of new records and recaptures (for a discussion of the *intimidation factor* see Brown 2008; we referred to this as *investigator effect* in Fitch and Pisani 2006). In the 54 years prior to 2003, HSF collected a total of 151 Timber Rattlesnake



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Fig. 1. Female *Crotalus horridus*, second recapture in 14 months on 11 June 2006, 910 mm SVL, 506 g, Jefferson County, Kansas. Segments 11 + button. Note two copper wires on rattle secured to mark string at this capture and 22 April 2006. This female added 2 segments and 50 mm SVL from 15 April 2005–22 April 2006. She had moved ~190 m east, contained 8 embryos, and added one segment (and 30 mm SVL) since April 2006.



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Fig. 2. Male *Crotalus horridus*, first recapture after 24 years on 22 May 2002, 1,200 mm SVL, 1,600 g, Jefferson County, Kansas. Segments 10, with many missing. Marked by HSF on 14 October 1978 at 995 mm SVL, segments 7 + button (see Fitch and Pisani 2002).

records from these same properties, whereas in the years 2003–2009, we have added 228 additional records. In our present database of 379 records, 123 are recaptures.

W.H. Martin (pers. comm. to GRP, October 2009) suggested the qualified applicability of Base50 Growing Degree Days (Base50-GDD) to *C. horridus* growth comparisons throughout the range of the species. He indicated that, as Base50-GDD is an agricultural metric and therefore plainly not by itself a sole determinant of *C. horridus* activity, a model incorporating such data should be explored. Correlations exist in many areas, suggesting that the abundant local Base50-GDD data available throughout the range of the species could be useful for approximating seasonal activity.

Growing degree day accumulations involve the amount of accumulated heat required for organisms to engage in normal metabolic life-cycle events (feeding and digestion, courtship, etc). Calculations of the Base50 growing degree day for a 24-hour period involve the following formula: $\text{Maxtemp} + \text{Mintemp}/2 - \text{Base temp (e.g., 50)} = \text{GDD}$. For a more extensive example, see: www.wunderground.com/about/faq/degreedays.asp.

The goals of this study were to revisit our conclusions in Fitch and Pisani (2006) and to compare the growth correlations mentioned therein with subsequent data from longer-term recaptures in the same population.

Methods

Data from the 59 records (largely recaptures) accumulated since Fitch and Pisani (2006) allow a more accurate assessment of growth, especially the

rapid growth shown by snakes of both sexes bearing rattles of up to button + 4 segments. We combined data on snakes with known growth histories with similar data collected since 1948 (Fitch Archive Database, Kansas Biological Survey). We then plotted and compared growth rates of male and female *C. horridus* to a generalized model of pit viper growth (Beaupre 2002), as well as to our 2006 papers.

When possible, we examined prey and compared sizes of prey taken with those of snakes. We palpated females to determine the presence of enlarged ovarian follicles.

We examined the potential seasonal activity of *C. horridus* in this small population using the regional data for Base50-GDD (between 1 March and 19 October, typically the limits of adult *C. horridus* activity at our site), and used repeated measures ANOVA to compare that to Base50-GDD over equivalent time periods in several eastern portions of the species’ range, where growth is far more gradual (Table 1). Our values are from NOAA airport databases (NOAA—National Climatic Data Center, www.airnav.com/airports/, last accessed 31 October 2009) at the localities in Table 1. We used the FAA Identifier to extract data from NOAA databases through Weather Underground (www.wunderground.com/history/airport/, last accessed 31 October 2009). Selecting the Custom tab and then specifying the dates retrieved the needed data. Base50-GDD data examined were for years 2003, 2004, 2008, and 2009. We began our detailed study of these snakes in 2003, which was characterized by typical spring and fall weather and an exceptionally warm dry summer. The following year was somewhat cooler, with considerably more precipitation (998 mm in 2004 versus 647 mm in 2003). Years 2008 and 2009 were the most recent years of our ongoing study. We used StatView software (Abacus Concepts 1991) to conduct statistical tests and produce graphical representations.

Results and Discussion

Local Potential Activity Season.—*Crotalus horridus* at our site experiences a significantly (Repeated Measures ANOVA; $p < 0.01$) longer potential activity season than at four comparison sites: two eastern localities at approximately the same latitude as Lawrence, and two from more northerly latitudes (Table 2; Fig. 3). All paired comparisons except MRB versus CKB differed significantly ($p = 0.05$). In general, the Base50-GDD decreases significantly and clinally to the northeast. We emphasize our agreement with W.H. Martin (pers. comm., 2009) that this metric, although useful for geographically broad comparisons, is not definitive for snakes that routinely thermoregulate behaviorally (see discussion in Huey 1991).

Feeding.—Fitch (1999) attributed the bulk of *C. horridus* prey biomass to larger rodents or lagomorphs, although he acknowledged that only the largest snakes (primarily males) fed on subadult Cottontails (*Sylvilagus*) or adults of genera of local larger rodents like *Sigmodon*, *Neotoma*, and *Sciurus*. However, given the small sample size (14 snakes

Table 1. Locations chosen for Base50-GDD comparisons.

FAA Airport Identifier	Name & Location	Latitude/Longitude (NAD83 Datum)	Elevation
LWC	Lawrence Municipal	39.0111111	833 ft/253.9 m
	Lawrence, KS 66044	-95.2164722	(surveyed)
MRB	Eastern WV Regional/Shepherd Field	39.4019031	565 ft/172 m
	Martinsburg, WV 25405	-77.9846686	(estimated)
CKB	Clarksburg Municipal	39.2966389	1217 ft/370.9 m
	Clarksburg, WV 26330	-80.2280833	(surveyed)
MGJ	Orange County Regional	41.5099722	364 ft/111 m
	Montgomery, NY 12549	-74.2646389	(estimated)
GFL	Floyd Bennett Memorial Airport	43.3412222	328 ft/100.0 m
	Glens Falls, NY 12804	-73.6103056	(surveyed)

Table 2. Mean Base50-GDD by station and paired comparisons between stations (LSD= Least Significant Difference); * significant at p = 0.05, ** significant at p = 0.01, ns = not significant.

Location	Mean Base50-GDD	Standard Deviation	Standard Error
LWC	3684.25	233.9606	116.9803
MRB	3158.00	152.0855	76.0428
CKB	3026.50	169.3960	84.6980
MGJ	2579.25	58.6025	29.3012
GFL	2085.25	88.3794	44.1897

Paired Comparison	Mean Difference	Fisher LSD test	F-test
MRB vs. MGJ	578.75	**	**
MRB vs. GFL	1072.75	**	**
MRB vs. LWC	-526.25	**	**
MRB vs. CKB	131.50	ns	ns
MGJ vs. GFL	494.00	**	**
MGJ vs. LWC	-1105.00	**	**
MGJ vs. CKB	-447.25	**	*
GFL vs. LWC	-1599.00	**	**
GFL vs. CKB	-941.25	**	**
LWC vs. CKB	657.75	**	**

of varying sizes in Fitch 1999), biomass may not be the best indicator of prey significance.

Although the number of identifiable stomach samples in our most recent data still is not large (28 of 379 snakes [7.4%] examined since 1948 contained 30 identifiable prey items), our data indicate that adults of rodent genera such as *Microtus* and *Peromyscus* are a dietary staple of adult *C. horridus* in this location. This is consistent with the broader studies of Clark (2002), among others. We earlier (Pisani and Fitch 2006) indicated that



Fig. 3. Old dark-phase male Timber Rattlesnake from Washington County, New York (estimated SVL 1,200 mm); the rattle has 16 segments with many missing (photographed in September 2007).

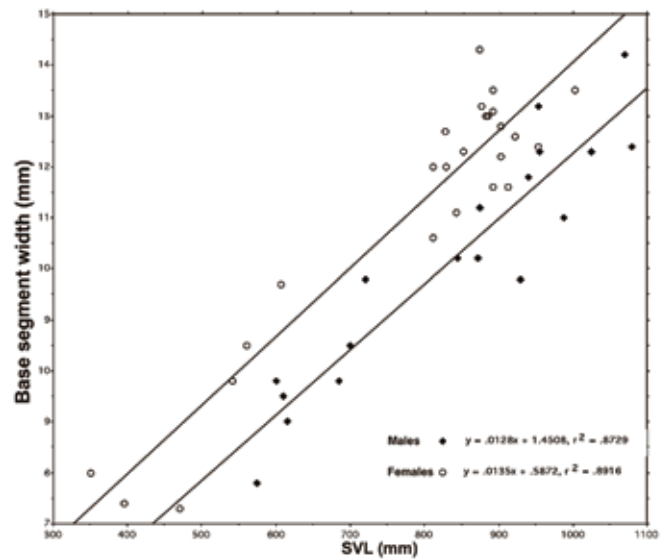


Fig. 4. Male and female SVL versus rattle base segment width and regression equations for *Crotalus horridus*, Jefferson County, Kansas with known growth histories.

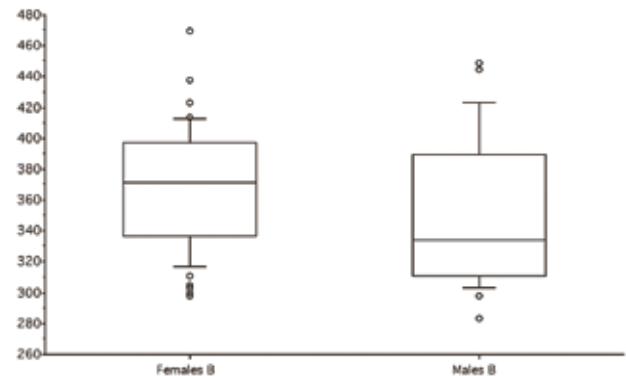


Fig. 5. SVLs (mm) compared for button-only stage female (n = 52) and male (n = 25) *Crotalus horridus*, Jefferson County, Kansas.

the structural complexity of the habitat utilized by our *C. horridus* population probably contributes to an abundant prey base. Such complexity has been reviewed for *Peromyscus leucopus* in a different locale by Anderson et al. (2003); their highest *P. leucopus* densities were in such habitat. Of the 30 identifiable prey items in our cumulative sample through 2009, 21 (70%) were microtines or soricids (*Blarina*, *Cryptotis*) found in 19 records with snake SVL range of 370–1,100 mm. The 9 “large prey” (*Sigmodon*, *Neotoma*, and *Sciurus*) were found in snakes 883–1,270 mm SVL (6 of the 9 with SVL > 1,000 mm). Most (234 of 330) *C. horridus* records in this area have been of snakes ≤ 900 mm SVL.

Given the relatively long potential activity season of our population, the opportunity for neonates to feed and assimilate a meal prior to hibernation cannot be discounted. Nor can this be conclusively established, as just one of our neonates (female, 370 mm SVL) contained prey (*Cryptotis*). Martin (2002) stated that neonates in his High Allegheny Plateau population of *C. horridus* did not feed until the following spring.

Growth and Age at Maturity.—Male and female sizes as correlated with rattle base segment width change equivalently with age (slopes are insignificantly different, p = 0.05; Fig. 4). Average sizes at varying growth stages differ from our 2006 data with the addition of these new records (Table 3). SVLs of sexes in this population are neither significantly different at the “button-only” stage (Fig. 5), nor at subsequent stages of growth (Table 3, Fig. 6). Comparison of our Table 3 with similar data in Martin

Table 3. Rattle segments and mean SVL (mm) for male and female *Crotalus horridus* in Jefferson County, Kansas.

Males Segments	Mean (n; range; SE)	Females Segments	Mean (n; range; SE)
Button only	351.04 (25; 283–449; 9.58)	Button only	367.23 (52; 298–470; 5.34)
1 + button	492 (3; 464–530; 19.70)	1+ button	438.5 (2; 382–495; 56.5)
2 + button	587.17 (12; 525–632; 10.46)	2+ button	569.7 (10; 520–610; 8.18)
3 + button	643.75 (11; 570–712; 14.91)	3+ button	631.71 (7; 570–718; 19.19)
4 + button	723.25 (8; 647–816; 19.43)	4+ button	706 (4; 504–807; 69.23)
5 + button	769.25 (4; 658–845; 41.03)	5+ button	810 (2; 810; 0)
6 + button	753.25 (4; 716–800; 17.99)	6+ button	789.0 (11; 644–900; 27.69)
7 + button	894.75 (4; 820–999; 37.52)	7–11+ button	914.25 (4; 890–957; 14.82)
8 + button	864.6 (5; 790–921; 21.18)		
9–15 + button	1,000.75 (4; 910–1170; 60.14)		

(2002: Table 5) indicates that snakes in this Kansas population generally grow faster through rattle stages 5 + button (Fig. 7). However, not all snakes are able to attain maximal growth despite generalized prey abundance and a generally favorable thermal regime. Five of our snakes were at stage 1 + button (all taken in different years), and four of those were captured in June–July; the fifth (female, 495 mm SVL) was an October capture and likely was completing her first full season.

Our few snakes with known growth histories since their birth years confirm the rapid potential growth of neonates as reported in Pisani and Fitch (2006). Those data, combined with our new records for snakes bearing complete rattles, allow a more accurate picture of rattle segment number and growth in this population (Table 3), revising our results in Fitch and Pisani (2006: Table 3). For example, a female (646 mm SVL at first capture) added 72 mm SVL and one rattle segment from April–September 2003. Another female, born fall 2002 and marked (button only, 403 mm SVL) in April 2003, gained 487 mm SVL and had added 9 segments (average 54 mm per segment) when killed by a vehicle at the field station in September 2006. Through that time, she had added an average of three rattle segments per year and an average annual SVL increase of 162 mm. A third female (605 mm SVL in April 2006, segments 3 + button) had grown to 810 mm SVL by May 2009 and added five segments (average 41 mm per segment). These three females averaged an increase in SVL of 56 mm



Fig. 7. Rattle of young male *Crotalus horridus* (715 mm SVL), DOR, Jefferson County, Kansas, 8 September 2006. Rattle has 3 + button segments.

per rattle segment. Two other young snakes collected in May 2009 (both at rattle stage 2 + button) had SVLs of 550 mm (male) and 520 mm (female); an April 2006 female in the same 2 + button class measured 560 mm SVL.

Our four smallest females known to contain enlarged ovarian follicles averaged 822 mm SVL (range 803–834 mm). The smallest of these (five enlarged follicles) had eight rattle segments, with an indeterminate number missing. Another measuring 820 mm SVL had a 12-segment rattle lacking just the button. The five females having both enlarged ovarian follicles and complete rattles averaged 868 mm SVL (range 820–890 mm) with rattles averaging 7.6 (+ button) segments.

Cumulatively, these observations indicate that females in this population may readily add three segments per year through their third year and will have the potential to mate that year and bear a first litter during their fourth year, consistent with our earlier inference (Fitch and Pisani 2006). Taylor and DeNardo (2008) and Beaupre (2008) reviewed the relation among foraging success, growth (increased SVL), and reproductive effort in (respectively) *Crotalus atrox* and *C. horridus*. Evaluating our data in light of these studies supports our conclusion that female *C. horridus* in our population generally experience high foraging success.

In Table 4, we have added pooled button-only (indicated simply as “B”) records (Fitch Archive Database, Kansas Biological Survey) to our most recent records of snakes with known growth histories. Not unexpectedly, the great preponderance of B records are concentrated in the fall (September–November). However, 18.4% (9 of 49) female B records are

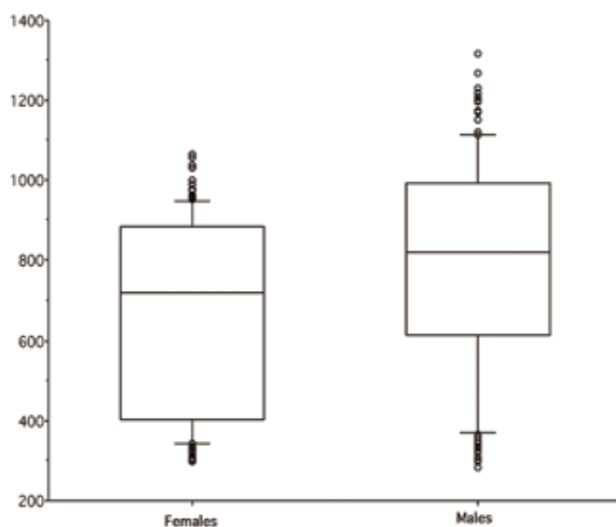


Fig. 6. Absence of significant sexual size dimorphism in *Crotalus horridus* from Jefferson County, Kansas. Females: mean \pm SE 664.93 \pm 18.86 mm (n = 163; r = 298–1065); males: Mean \pm SE 791.42 \pm 20.41 mm (n = 167; r = 283–1318).

Table 4. Distribution of rattle segment classes by sex and month of *C. horridus*, Jefferson County, Kansas. B = button.

April	May	June	July	August	September	October–November
Males						
3 + B (n = 5)	2 + B (n = 2)	1 + B (n = 1)	1 + B (n = 2)	2 + B (n = 1)	B (n = 7)	B (n = 12)
4 + B (n = 1)	3 + B (n = 1)	2 + B (n = 1)	3 + B (n = 1)	4 + B (n = 1)	2 + B (n = 3)	2 + B (n = 4)
5 + B (n = 1)	4 + B (n = 2)	3 + B (n = 2)	6 + B (n = 1)	8 + B (n = 1)	3 + B (n = 1)	3 + B (n = 1)
6 + B (n = 1)	5 + B (n = 1)	7 + B (n = 2)	7 + B (n = 1)		5 + B (n = 1)	4 + B (n = 4)
8 + B (n = 2)	10 + B (n = 1)		8 + B (n = 1)		6 + B (n = 1)	5 + B (n = 1)
	12 + B (n = 1)				7 + B (n = 1)	6 + B (n = 1)
					8 + B (n = 1)	
					9 + B (n = 1)	
					15 + B (n = 1)	
Females						
B (n = 9)	B (n = 3)	B (n = 1)	6 + B (n = 1)	B (n = 1)	B (n = 15)	B (n = 20)
2 + B (n = 2)	2 + B (n = 2)	1 + B (n = 1)		2 + B (n = 3)	5 + B (n = 1)	1 + B (n = 1)
3 + B (n = 1)	3 + B (n = 2)	3 + B (n = 1)		4 + B (n = 1)	7 + B (n = 1)	2 + B (n = 3)
6 + B (n = 3)	6 + B (n = 2)	4 + B (n = 1)		5 + B (n = 1)	9 + B (n = 1)	3 + B (n = 3)
8 + B (n = 1)		6 + B (n = 3)		6 + B (n = 1)		4 + B (n = 2)
		11 + B (n = 1)				

in April, with 10% (5 of 49) more recorded in the months of May, June, and August. As elaborated above, not all snakes are able to attain maximal rate of growth. Although 100% of male B records (n = 19) are fall-only, we presently feel that this is an artifact of the greater number of females in our sample.

Growth Rate and Models.—Beaupre (2002) presented a generalized model of pit viper growth. Underlying assumptions of the model are: (1) Large, infrequent meals, and (2) abrupt asymptotic reallocation of resources from growth to reproduction in females. The model was not intended to be all-inclusive, and did not consider such factors as an energy value for female annual maintenance activities (i.e., foraging to accumulate sufficient energy reserves for daily activity or for successful hibernation). Beaupre (2002) stated that: “It seems clear that food availability and temperature interact in complex ways to affect growth.”

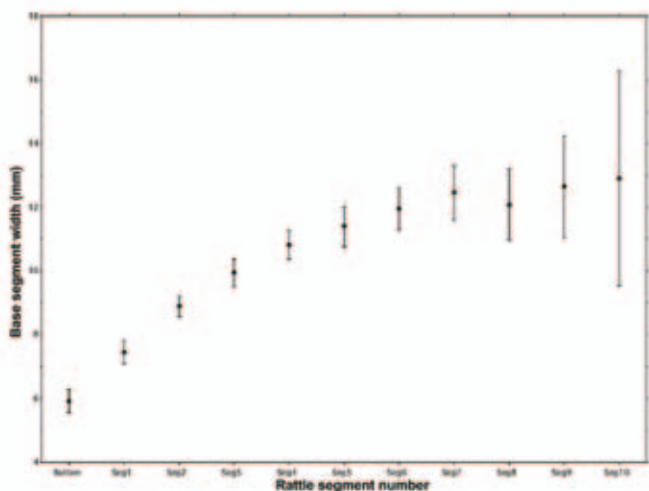


Fig. 8. Means and 95% confidence bars of rattle segments from *Crotalus horridus*, Jefferson County, Kansas with known growth histories (sample sizes as in Fig. 4).

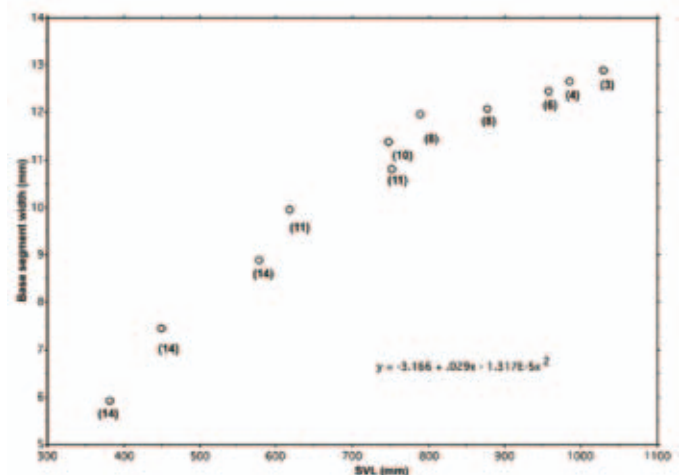


Fig. 9. Growth trajectory and 2nd-order polynomial equation for *Crotalus horridus*, Jefferson County, Kansas (circles are mean base segment width versus SVL, parenthetical numbers are sample sizes).

Older females in our population, as predicted by Beaupre’s (2002) model, seem to cease their rapid early SVL increase (Table 3), although ecdysis may remain frequent. One example is an 840-mm SVL female (rattle stage 8 + button, April 2005) that had added just 70 mm SVL by June 2006, but four rattle segments (average 17.5 mm per segment).

Using our data from 2006–2009 (pooled sexes) of snakes with complete (button present) rattle strings or snakes with known growth histories, we plotted increases in SVL and width of base rattle segment (Figs. 8 & 9). The best-fit second-order polynomial regression of those data (Fig. 9) using mean values at each rattle segment is favorably comparable to the “tree rings” plot of our data in Fitch and Pisani (2006, Fig. 8), giving us increased confidence in our 2006 conclusions. Pooled (male + female) growth trajectory data from our snakes (Figs. 8 & 9) seem to us to be most similar to that of males in Beaupre’s (2002) model, with higher Mean Foraging Success of 0.050–0.075 and a +4 to +8 °C thermal regime.

Conclusions

Our most recent data confirm the pattern of growth in this population of *C. horridus* noted in our 2006 papers (very rapid growth through the fourth post-button shed; Fig. 10). By that stage, males have attained an average SVL of 723 mm and females an average SVL of 706 mm. This would seem to be a result of the abundant prey base in a habitat mosaic, combined with a significantly longer average potential growing season than at eastern localities of the same latitude and similar altitudes, or at more northerly latitudes (Fig. 11).

Rapid growth facilitates earlier female reproduction in our population than *C. horridus* shows at parts of its range characterized by shorter growing seasons (Brown 1993, Martin 2002). A potentially longer activity season and a rich resource base also no doubt facilitate female accumulation of sufficient energy reserves to reproduce more frequently than in localities more limited in energy and/or thermal resources.

The growth curve presented by Fitch and Pisani (2006), although based largely on averaging rattle segment data and fitting snakes to presumptive size-age classes, accurately compares to the present more restricted calculations using only snakes with known growth histories and/or complete rattle strings. Continued studies will refine applicability of mathematical models to observed growth in this population.

We will continue to explore weather variables that are collected both locally and nationally and that, when combined with Base50-GDD, will allow better approximation of actual microclimates available to *C. horridus* in this population. The ability to use widely available historical weather data relevant to *C. horridus* life history would allow refinement of modeling through the range of the species.

Literature Cited

Anderson C.S., A.B. Cady, and D.B. Meikle. 2003. Effects of vegetation structure and edge habitat on the density and distribution of White-footed Mice (*Peromyscus leucopus*) in small and large forest patches. *Canadian Journal of Zoology* 81:897–904.

Beaupre, S.J. 2002. Modeling time-energy allocation in vipers: Individual responses to environmental variation and implications for populations, pp. 463–482. In: G.W. Schuett, M. Höggren, M.E. Douglas, and H.W. Greene (eds.), *Biology of the Vipers*. Eagle Mountain Publishing LC, Eagle Mountain, Utah.

Beaupre, S.J. 2008. Annual variation in time-energy allocation by Timber Rattlesnakes (*Crotalus horridus*) in relation to food acquisition. pp. 111–122.



Fig. 10. Male *Crotalus horridus* (Douglas County, Kansas), August 2006. Estimated SVL 1,000 mm, rattle has 6 segments with many missing.



Fig. 11. Female yellow-phase *Crotalus horridus* (Washington County, New York), September 2007. Estimated SVL 600 mm, rattle has 7 + button segments. This snake is considerably older than a female from Jefferson County, Kansas at a comparable rattle stage.

In: W.K. Hayes, K.R. Beaman, M.D. Cardwell, and S.P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California.

Brown, W.S. 1993. *Biology, Status, and Management of the Timber Rattlesnake (Crotalus horridus): A Guide for Conservation*. Herpetological Circular No. 22. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri.

Brown, W.S. 2008. Sampling Timber Rattlesnakes (*Crotalus horridus*): Phenology, growth, intimidation, survival, and a syndrome of undetermined origin in a northern population, pp. 235–266. In: W.K. Hayes, K.R. Beaman, M.D. Cardwell, and S.P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, California.

Clark, R.W. 2002. Diet of the Timber Rattlesnake (*Crotalus horridus*). *Journal of Herpetology* 36:494–499.

Fitch, H.S. 1999. *A Kansas Snake Community: Composition and Changes Over 50 Years*. Krieger Publishing, Malabar, Florida.

Fitch, H.S. 2002. A comparison of growth and rattle strings in three species of rattlesnakes. *Scientific Papers (Natural History Museum, University of Kansas)* 24:1–6.

Fitch, H.S. and G.R. Pisani. 2006. The Timber Rattlesnake in northeastern Kansas. *Journal of Kansas Herpetology* (19):11–15.

Fitch, H.S. and G.R. Pisani. 2002. A natural longevity record for the Timber Rattlesnake (*Crotalus horridus*). *Journal of Kansas Herpetology* (3):15–16.

Huey, R.B. 1991. Physiological consequences of habitat selection. *American Naturalist* 137 (Supplement):S91–S115.

Klauber, L.M. 1956. *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. University of California Press, Berkeley.

Martin, W.H. 2002. Life history constraints on the Timber Rattlesnake (*Crotalus horridus*) at its climatic limits, pp. 285–306. In: G.W. Schuett, M. Höggren, M.E. Douglas, and H.W. Greene (eds.), *Biology of the Vipers*. Eagle Mountain Publishing LC, Eagle Mountain, Utah.

NOAA—National Climatic Data Center. 2009. www.ncdc.noaa.gov/oa/documentlibrary/hcs/hcs.html.

Pisani, G.R. and H.S. Fitch. 2006. Rapid early growth of Timber Rattlesnakes in northeastern Kansas. *Journal of Kansas Herpetology* (20):19–20.

Taylor, E.N. and D.F. DeNardo. 2008. Proximate determinants of sexual size dimorphism in the Western Diamond-backed Rattlesnake (*Crotalus atrox*), pp. 91–100. In: W.K. Hayes, K.R. Beaman, M.D. Cardwell, and S.P. Bush (eds.), *The Biology or Rattlesnakes*. Loma Linda University Press, Loma Linda, California.

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