Review Article

Relationship of environmental temperatures and activity of *Chelydra serpentina* in Southeastern Pennsylvania, USA

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ABSTRACT – Thermal ecology and daily and annual activity periods of the turtle *Chelydra serpentina* were studied from 1964-1992 in southeastern Pennsylvania, USA. Turtle activity and related cloacal body temperature (BT) were most influenced by the temperature of the medium the turtle experienced; water temperature when aquatic (WT, r = 0.92) or air (AT, r = 0.87) when on land. Most captures were aquatic. Annually turtles were active after emergence from hibernation in early March, and remained active until reentering hibernacula in early October. Daily activity normally lasted from about 07:00 h to when it became too dark to locate the animals. Most activity occurred between 08:00-13:00h, but some crepuscular or nocturnal foraging activity occurred as some turtles were found in the morning in traps that had been freshly baited the evening before. Also, some nesting females oviposited after dark or during the crepuscular morning hours. Activity on land was essentially restricted to nesting females.

INTRODUCTION

Body temperature data from free living *Chelydra serpentina* in the MidAtlantic region of the USA are generally lacking, as most studies of its temperature tolerances have been conducted in laboratories using controlled thermal gradients. The data we report offer a valuable comparison to previous studies; and are comparative also as baseline data for other populations of *C. serpentina* in the MidAtlantic region.

The main purposes of this study were to determine the thermal ecology of the snapping turtle, *C. serpentina*, at a southeastern Pennsylvania pond/marsh complex, and to calculate the turtle's operating body temperature (OBT) range for several daily and annual behaviours at the site for comparison with other such data from previously published studies conducted farther north or south of Pennsylvania.

MATERIALS AND METHODS

Snapping turtles were studied during over 1,000 collecting trips from 1964 to 1992 at the White Oak area, a 2.5 ha soft-bottomed mill pond bounded by 10 ha of mixed marsh and woodland habitat formed by the damming of Big Chickies Creek, a tributary of the Susquehanna River, slightly more than 2 km north of Manheim, Lancaster County, Pennsylvania. The site is described in detail in Ernst (1969, 1971). All research and collection of turtles at White Oak was covered by annual permits from the Pennsylvania Fish Commission, including the years 1964-1992.

The site supported a variety of vertebrates, particularly migratory waterfowl. Other turtles present were the aquatic *Chrysemys picta*, *Clemmys guttata*, *Glyptemys insculpta*, *G. muhlenbergii*, *Sternotherus odoratus*, and the

Category	ВТ	AT	ST	WT
All capture records (331)	21.8 ± 4.9	23.0 ± 4.7	23.7 ± 5.2	20.7 ± 4.6
	(4.0-34.0)	(6.0-33.0)	(5.0-34.0)	(4.0-30.0)
		r = 0.87	r = 0.87	r = 0.92
Adult females	22.1 ± 5.2	22.2 ± 4.9	22.9 ± 5.5	20.2 ± 4.4
	(4.0-30.0)	(8.0-33.0)	(8.0-34.0)	(4.0-27.0)
		r = 0.88	r = 0.90	r = 0.92
Adult males	21.0 ± 5.7	22.5 ± 5.3	23.3 ± 5.6	20.3 ± 5.4
	(4.0-34.0)	(6.0-30.0)	(5.0-33.0)	(4.0-28.0)
		r = 0.91	r = 0.89	r = 0.96
Immatures	22.6 ± 3.5	23.9 ± 3.7	24.6 ± 4.6	21.6 ± 3.6
	(12.0-30.0)	(12.0-31.0)	(6.0-34.0)	(10.0-30.0)
		r = 0.78	r = 0.82	r = 0.86

Table 1. Relationships of cloacal body temperature and environmental temperatures of common snapping turtles, *C. serpentina*, presented as means and ranges, in Lancaster County, Pennsylvania: cloacal body temperature (BT), air temperature (AT), land surface temperature (ST), water temperature (WT), standard deviation (SD), correlation coefficients (r) with BT. All temperatures in degrees Celsius.

terrestrial *Terrapene carolina* in the woodlands. The population of *Chelydra* was more scattered and smaller than those of the more populous *C. picta*, *C. guttata*, and *S. odoratus* (Ernst, 1971).

During the study, 280 *C. serpentina* (adult males, 118, 41.9%; adult females, 60, 21.5%; and immatures, 102, 36.6%) were captured a total of 331 times. The minimum CLs of captured White Oak mature males and mature females were 204 mm and 271 mm, respectively; based on the tail length and anal vent position sexual dimorphism reported by Ernst & Lovich (2009).

Adult and larger immatures were livetrapped in six hoop-net traps baited with canned or fresh fish, bovine liver, or chicken entrails at seven pond stations where turtles were seen to bask or feed (Ernst, 1965). The traps were checked and rebaited daily in the early morning and late afternoons. Smaller individuals in the shallow marsh or brooks were captured by hand or with a dip net. Hibernating snapping turtles were located either by hand muddling in the soft bottoms of the shallow waterways or by using the long-pole technique known as "sounding" in deeper waters (Carpenter, 1955).

At each capture, the date, 24-h military time, location, and, except for trapped individuals, the turtle's behaviour were recorded. All *Chelydra* were sexed, aged, measured, weighed, and individually shell notched for future identification (Ernst et al., 1974; Ernst & Lovich, 2009). The straight-line carapace length (CL) was measured with dial calipers accurate to 0.1 mm, and mass was determined using a triple-beam balance. Algal colonies and leeches present on the turtle were identified and counted (Ernst et. al., 2012).

The turtle's cloacal body temperature (BT) was taken with a Schultheis cloacal thermometer accurate to 0.1 °C. Also recorded with a multichanneled Yellow Springs quick-reading telethermometer accurate to 0.2 °C were the air temperature (AT) 10 cm above the capture point, and, at the exact capture point, the surface temperature (ST) if terrestrial, or water temperature (WT) at a depth of 10 cm if aquatic.

All data were statistically analyzed using R, Version 2.15.2; levels of significance were set a priori at $\alpha = 0.05$. Analysis was by correlation coefficient, and by ANOVA using Tukey's multiple comparisons.

Capture data were plotted using violin plots. These plots are essentially box plots modified by using a kernel smoother. The relative thickness of the plotted area represents the relative number of animals, both within and between the different groups.

RESULTS AND DISCUSSION

Body Temperature

Temperature data recorded during 331 captures of *C. serpentina* at White Oak are reported in Table 1. Anova comparisons followed by

Environmental temperatures and activity of Chelydra serpentina

BT	AT	ST	WT
22.3	24.8	25.0	21.3
(5.0-30.0)	(10.0-30.0)	(12.0-34.0)	(5.0-30.0)
22.3	22.9	22.9	20.4
(16.0-26.0)	(18.0-30.0)	(18.0-33.0)	(16.0-25.0)
24.9	23.1	22.8	21.1
(15.0-34.0)	(12.0-30.0)	(12.0-31.0)	(10.0-26.0)
21.5	23.0	24.0	20.5
(17.0-26.0)	(20.0-26.0)	(20.0-28.0)	(15.0-26.0)
24.1	26.2	26.0	23.4
(20.0-29.0)	(14.0-31.0)	(18.0-32.0)	(18.0-28.0)
22.6	21.6	21.7	19.3
(18.0-30.0)	(17.0-29.0)	(17.0-30.0)	(16.0-26.0)
16.0	20.0	20.0	16.0
6.3	9.3	9.5	6.1
(4.0-12.0)	(6.0-14.0)	(5.0-10.0)	(4.0-12.0)
21.0	23.0	23.8	20.0
(16.0-24.0)	(17.0-29.0)	(18.0-31.0)	(16.0-22.0)
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Table 2. Relationships of cloacal body temperature of *C. serpentina* to behaviour presented as mean and range: number of records (N), cloacal body temperature (BT), air temperature (AT), land surface temperature (ST), water temperature (WT); all temperatures in degrees Celsius.

Tukey's multiple comparisons between the BTs, ATs, STs, and WTs of the sex/age classes of adult males, adult females and immatures indicated that significant differences were present between the three classes in the mean temperatures of AT (P=0.0327) and ST (0.0297) but not between their BTs and WTs. Correlation coefficients (r) for BT versus WT also showed the highest correlations in all three classes with values above 0.90, indicating that WT was the most important ectothermic influence at the time of capture on all three sex/age groups.

Separate ANOVA comparisons were also performed of BT to AT, ST and WT for the individual adult sexes and immature as were separate additional Tukey's multiple comparisons to tease apart the separate temperatures for these three groups. For adult males, WT was significantly different from both AT and ST, and BT was significantly different from ST. WT is the most important thermal source for males, as indicated by the correlation coefficient (r), as adult males were more highly aquatic and less often captured on land than adult females. The same relationships

occurred in immatures, as they too spend the greatest amount of time in water. During the nesting season in late May and June, ovipositing females spend considerable time on land, causing a significant difference between WT and ST. These differences indicate that *Chelydra* of all sexes and ages are influenced most by the warmest medium in which they are in contact.

Few comparative literature reports of field environmental temperatures (ETs) at the time and point of capture of *Chelydra* are available, and these are almost exclusively from localities farther north or south of our research site. Brown et al. (1990) noted that the mean BT of eight free-ranging Ontario, Canada, C. serpentina was 22.7 °C at a mean corresponding ET of 24.9 °C. Knight et al. (1990) reported that Ontario hatchlings placed in a laboratory thermal gradient selected a similar ET. In a second Ontario study, Brown et. al. (1994) reported that the mean radio telemetry recorded BTs and ETs of snapping turtles at two principal sites were: BT 19.5 °C and 22.5 °C, WT 19.5 °C and 22.6 °C, and AT 16.8 °C and 20.4 °C, respectively; and Obbard & Brooks (1981) and

Species	BT	AT	ST	WT	Source
Chelydra ser- pentine	21.8	23.0	23.7	20.7	Present study
	(4.0 - 34.0)	(6.0-33.0)	(5.0-34.0)	(4.0-30.0)	
Chrysemys picta	22.2	25.8	27.5	16.2	Ernst, 1969, 1972
	(4.5-34.0)	(8.0-29.0)	(3.8-41.0)	(4.0-21.5)	
Clemmys gut- tata	20.2	20.2	19.4	16.6	Ernst, 1982
	(3.0-32.0)	(0.0-30.0)	(4.0-32.0)	(2.0-32.0)	
Glyptemys insculpta	21.0	21.9	20.2	17.4	Ernst, 1986a
	(3.5-30.1)	(3.0-35.0)	(4.0-33.0)	(5.6-28.0)	
Glyptemys muhlenbergii	20.3	22.0	21.8	18.4	Ernst, 1977
	(16.2-31.0)	(17.0-23.4)	(19.4-24.1)	(15.0-22.8)	
Sternotherus odoratus	21.7	23.3	21.4	20.2	Ernst, 1986b
	(14.0-30.0)	(4.2-32.0)	(9.0-28.5)	(3.8-30.0)	

Table 3. A comparison of temperature relationships (presented as mean and range) of the six aquatic turtles at White Oak, Pennsylvania; all temperatures in degrees Celsius: cloacal body temperature (BT), air temperature (AT), land surface temperature (ST), and water temperature (WT).

Brown & Brooks (1991) stated that Ontario *Chelydra* were active at WTs of 7.5-28.8 °C. Punzo (1975) reported Florida *C. s. osceola* had a WT activity range of 18.7-32.6 °C. In another Pennsylvania study farther east, at approximately the same latitude, near Philadelphia, active *Chelydra* were found in water of 5-33 °C (Saba, 2001). At Mason Neck, 268 (95.7%) of the WTs of active snapping turtles were 16-26 °C, falling between the preceding reports.

Most White Oak BTs fell between 15.0-27 °C (n = 222, 67.1%); and WTs between 10-30 °C. Other pertinent ranges were: 20-26 °C (n =173, 52.3%). 22-26 °C (n = 133, 46.2%), and 24-26 °C (n = 93, 28.1%). These field records indicate the most normal BT for naturally active White Oak Chelydra lies between 20-26 °C, the turtle's operating body temperature (OBT) range at White Oak; a range lower than the mean selected temperature of this species and other aquatic turtles in laboratory studies using thermal gradients (Schuett & Gatten, 1980; Williamson et al., 1989; Nutting & Graham, 1993; Bury et al., 2000). However, the BTs of wild White Oak Chelydra were recorded throughout the annual activity period of the turtle at various ETs while the laboratory studies were conducted with acclimated individuals under controlled laboratory temperatures (additional laboratory thermal data are reported in Spotila & Bell, 2008). Temperatures selected in previous laboratory thermal gradients are more properly termed preferred body temperatures (PBT) as opposed to OBT, which is strictly a field measurement.

The recorded BTs of Mason Neck Chelvdra are closely correlated with corresponding ETs. None of these BT ranges approach the reported mean critical thermal maximum (CT_{max}) for young Chelydra of 39.1 °C acclimated to 15 °C and 41.1 °C for those acclimated to 25 °C in laboratory thermal gradients by Williamson et al. (1989). Similarly, Hutchison et al. (1966) reported a mean CT_{max} of 39.5 °C (37.4-40.6 °C) for various age/size snapping turtles acclimated in constant temperature chambers. Baldwin (1925) noted that in the laboratory Chelydra subjected to an ET of 41.2-44.5 °C had cloacal BTs of 33.5-39.0 °C and were in severe distress, but recovered when cooled. Brattstrom (1965) had previously noted minimum and maximum voluntary field BTs of 5.0 °C and 24.5 °C for a single individual. Boyer (1965) reported that Chelydra in full



Figure 1. Violin plot of annual activity periods by months of adult male, adult female, and immature *C. serpentina* at White Oak, Lancaster County, Pennsylvania.

sunlight reached BTs of close to 38 °C, indicating, in view of the above studies, why *Chelydra* seldom basks out of water (Ewert, 1976).

The cloacal BT activity range of Florida *C.* serpentina was 18.7-32.6 °C (Punzo, 1975); while the mean field BTs of active and inactive Ontario snapping turtles were 19.5-21.7 °C and 18.9-20.8 °C, respectively (Obbard & Brooks, 1981), and live gravid females buried in an Ontario wood chip pile did not survive after the AT reached 31.8 °C (De Solla et al., 2001). The MidAtlantic BTs from White Oak present a useful comparison with these records from the extreme southern and northern limits of the species range.

The highest BTs recorded for White Oak *Chelydra* were from three basking adults at 30-34 °C; a nesting female, 30 °C; and another traveling overland to nest, 30 °C. Brown et al. (1990) reported that basking Ontario snapping turtles maintained a mean BT of 28-30 °C.

While *C. serpentina* can exercise behavioural control of its BT by seeking a cooler temperature regime when experiencing high ETs, it has little control over lower ETs during winter and becomes torpid. Although many data are available on the critical thermal minimum (CT_{min}) tolerated by hatchlings in thermal laboratory studies (Ernst & Lovich, 2009), the reported field BTs of cold dormant snapping turtles are rare and do not approach those recorded in laboratory tests. White Oak *Chelydra* normally avoided extreme winter ETs by selecting well insulated hibernation sites (see below). Brattstrom (1965) gave 5 °C as the



Figure 2. Violin plot of daily activity period by 24-hour (military) time of adult male, adult female, and immature *C. serpentina* at White Oak, Lancaster County, Pennsylvania.

lowest BT for activity of this turtle, while Obbard & Brooks (1981) noted that Ontario individuals became active at 7.5 °C, and captives kept in an outdoor enclosure in Germany by Hass (1985) became active at 9 °C. In Ohio, *Chelydra* buries into soft aquatic bottoms when the WT drops to 15 °C, possibly because it ceases to feed at this WT or cooler (Meeks & Ultsch, 1990). The lowest BT recorded at White Oak in a similar hibernaculum was 4 °C (Table 2). Many aspects of the physiology of cooling in *Chelydra* and other species of North American turtles have been well studied by a variety of researchers (see Ernst & Lovich, 2009).

Comparative temperature data for the six aquatic turtle species at White Oak are presented in Table 3. The six species had a combined mean BT of 21.0 (3.0-31.0) °C. The most common basker, Chrysemys picta, exhibited a higher mean AT and ST than the others, probably due to its longer exposure to the sun and selection of more exposed aerial basking sites. C. serpentina did a minority of its basking while floating at the water surface with its dorsal carapace exposed, experiencing lower means of AT and nearby ST. Clemmys guttata, a known cool weather semiaquatic species, exhibited the lowest mean ETs; followed by the two semiterrestrial species of Glyptemys. None of these temperature differences were unexpected in view of the different species' normal microhabitat requirements and behaviours (Ernst & Lovich, 2009).

Behavioural Body Temperature Versus Environmental Temperatures

Ectothermic animals, such as turtles, must be warmed to a critical temperature from environmental sources before capable of any activity. Subsets of activity apparently have their own lower temperature thresholds and ranges, possibly due to seasonal effects; indications of these are reflected in Table 3 where the BTs and ETs of active White Oak *Chelydra* are reported. At White Oak *Chelydra* began to move in the water or over land, as indicated by either trapping or hand collection, at BTs and WTs of 5.0 °C (aquatic capture), and ceased moving when their BTs reached 34 °C. Obbard & Brooks (1981) reported similar overall BT and WT ranges for Ontario *Chelydra*.

Snapping turtles bask less out of water than do emydine species (Ewert, 1976), and some basking is achieved when floating at the water surface with the dorsal surface of the carapace exposed. The temperature regimes of these two basking classes at White Oak are shown in Table 3. One spring aerial basking Chelydra had a BT of 15 °C at an AT of 12 °C and WT of 10 °C; and an adult male achieved a BT of 34 °C at an AT of 30 °C, the highest BT recorded at White Oak. Basking Chelydra did not reach BTs near their reported CT_{max} of > 37 °C. Obbard & Brooks (1979) reported that the number of atmospheric basking Ontario Chelydra was positively correlated with total daily solar radiation and with maximum AT but negatively correlated with daily precipitation, and that maximum WT had little influence. Data and observations from White Oak are in agreement with their conclusions. The maximum recorded BT for the Ontario snapping turtles was also 34 °C, but their mean BT for atmospheric baskers was higher, 27.6 °C, than that of the 17 White Oak turtles. Both the Ontario and White Oak studies found that Chelydra basks out of water more often than implied by Ewert (1976). Aquatic basking at White Oak began at WTs as low as 15 °C, and the two captured basking on the water surface only attained a BT of 26 °C.

Aquatic North American turtles generally begin to feed at BTs and WTs of 16 °C (Ernst & Lovich, 2009), and *Chelydra* fits this pattern (Brown & Brooks, 1991); although Punzo (1975) reported the lowest BT for active Florida *C. s. osceola* was 18.7 °C where WTs are generally higher. At White Oak, the turtle was attracted to baited traps at WTs of 16 °C; although those actually observed feeding were in shallow water at BTs and WTs of 20 °C and 18 °C, respectively. Feeding continued from the spring until in late summer the WT reached 28 °C and the AT and adjacent ST 31-32 °C. *Chelydra* was later attracted to baited traps or observed to feed when the WT dropped again below 28 °C, but ceased when it fell to 17 °C.

Nesting at White Oak was observed from 31 May to 12 June. In southern Florida oviposition occurs as early as late February or March and in northern Florida it has been reported from early May until late June (Punzo, 1975; Ewert, 1976; Iverson, 1977; Aresco et al., 2006). White Oak nesting took place in both morning and evening under similar ETs; such a daily pattern of nesting has also been noted elsewhere for Chelvdra (Hammer, 1969, 1971; Ewert, 1976; Ernst et al., 1997; Iverson et al., 1997). Obbard and Brooks (1987) reported that Ontario females required at least 344 heat units/degree days based on a quantified summation of the daily maximum and minimum temperatures of the water in their habitat before initiation of oviposition (Arnold, 1960); this normally occurred in early June. The AT and ST ranges for White Oak nesters were 17-29 °C and 17-29 °C, respectively. Nesting females achieved BTs as high as 30°C.

Chelydra hibernate in winter. At White Oak, cessation of activity began when the autumn WT fell to 10 °C. The duration of winter activity usually extended from midOctober to midMarch; although in Ohio inactivity first occurs from late September and early October to as late as early November, and, in northwestern West Virginia, the mean date of entry into hibernation was 9 October and the mean emergence date was 13 April (Meeks & Ultsch, 1990; Strain et al., 2012). Virginia Chelydra are active from 19 March to 22 October (Bazuin, 1983). During extended warm winter periods some snapping turtles, although not observed at White Oak, may emerge and surface bask near their hibernaculum or move about (Meeks & Ultsch, 1990; Mitchell & Barrish, 1996; Ernst & Lovich, 2009).

Eight White Oak individuals were found buried in the soft bottom of waterways in

March with BTs of 4-12 °C (Table 3). The turtle with the highest BT (28 March) appeared to be digging its way out of its hibernaculum.

Four *Chelydra* (June: an adult male, an adult female, and a 175 mm CL juvenile; August: an adult female) were found in land forms when ETs were warm. It is not known if these turtles were seasonally estivating or had just spent the night on land, but the June female may have remained on land after nesting. Their mean BT was lower than both that of AT and ST, but more closely matched the nearby WT; indicating that possibly these turtles had just emerged from the water.

The temperature data presented in Tables 1 & 3 indicate that the BT of White Oak *Chelydra* is determined predominately by either the WT or AT, depending on how much of the turtle's body is exposed to the air.

Annual Activity Cycle

Active White Oak *Chelydra* were captured from 5 March to 8 October (217 days, Fig. 1), and, in all years of full time study, had a mean annual activity cycle of 173 days. Of 12 (3.6% of total captured turtles), found in March, 11 were inactive and either hibernating or in early arousal. The one surface active individual was moving in shallow water on 31 March. Only 21 *Chelydra* (6.3%) were considered active in April (including overwintered hatchlings). The earliest two surface active April *Chelydra* were found moving in shallow water on 1 April and basking at the water surface on 10 April. Two combating males were captured in shallow water on 14 April.

The most active period at White Oak (193 captures, 58.3%) was May-July, which included a nesting season from 31 May to 12 June. Nesting has occurred as early as 18 May in Florida to as late as 1 July in Maine, and peaks in Ontario in midJune (Coulter, 1958; Obbard & Brooks, 1981; Iverson et al., 1997). Activity (movements, foraging, and trapped animals) declined drastically for White Oak adults during August (16 captures, 4.8%), a trend we also saw in Virginia Chrysemys picta, that is apparently correlated with higher WTs. All eight turtles (2.4%) found in October were active, either moving (7) or basking (1). This pattern does not match the "unimodal" cycle reported for Pennsylvania C. serpentina by Hulse et al. (2001), although their most active period, June-July, falls within that exhibited by White Oak *Chelydra*.

The annual activity period at White Oak matches that reported for Virginia, but is shorter than the more extended annual period in North Carolina (Bazuin, 1984; Mitchell, 1994; Palmer & Braswell, 1995). Farther North, Maine *Chelydra* are active from late May into October, and those in southern Ontario from midMay to early October (Obbard & Brooks, 1981; Hunter et al., 1999).

White Oak adults of both sexes were equally active between emergence from hibernation and midMay after which females increase their activity until midJune during the nesting season. From July to cessation of annual activity in October, both sexes at White Oak had similar levels of activity. Such a sexually different annual activity period has been previously reported in Ontario *Chelydra* by Brown & Brooks (1993).

Daily Activity Cycle

The daily collection period normally lasted from approximately 07:00 h to when it became too dark in the evening to find turtles. Data on daily captures of Chelydra are presented in Fig. 2. The earliest was found at 0720 h, and only eight (2.4% of total captures) were detected before 0800 h. Most active turtles (208, 62.8%) were captured during 0:800-12:59 h; after this activity began to slow and four (1.2%) were found inactive in land forms. Although 28 (8.5%) of captured Chelydra were found between 13:00 h and 14:59 h, activity slowed after 13:00 h, with only 15 (4.5%) captured before 18:00 h. However, some crepuscular or nocturnal foraging must have occurred, as traps freshly baited in the late afternoon or early evening before contained Chelydra the next morning. Obbard & Brooks (1981) reported Ontario Chelydra crepuscular; and Smith & Iverson (2004) noted that most of their trap captures were made at dawn or early evening.

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