Annual and daily activity cycles of snakes in northern Virginia, USA

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The annual and daily activity cycles of North American reptiles are determined by physiological responses to both temperature and light; and are seasonal (Gibbons & Semlitsch, 2001). While many field studies of North American snakes have included data on seasonal activity patterns, their daily activity cycles have been mostly under reported in only general terms. This is the only long term study of a snake in the middle Atlantic region of the USA, and as such is valuable for comparison with other such North American research; and reports baseline information which may also be critical to future studies on the effects of global warming on snake communities.

Ecology of 16 snakes (Table 1) was studied at the Mason Neck National Wildlife Refuge, Fairfax County, Virginia, USA (38° 67' N, 77° 10' W, ~25-35 m elevation), from April 1982 to August 2006, but concentrated from 1990 to 2006 (Hartsell, 1993; Ernst et al., 1997; Creque, 2001; Orr, 2003, 2006). Calculations of the annual and daily activity cycles are reported below.

METHODS AND MATERIALS

Most snakes were collected by hand. Surveyor effort was as constant as possible from March through November. Data recorded at each snake encounter included sex and life stage (male, female, hatchling/newborn, juvenile or immature; Ernst & Ernst, 2003); total body length (TBL), snout-vent length (SVL) and tail length (TL, from vent to tip), measured with a cloth measuring tape (large snakes) or a standard metric ruler (small snakes); mass recorded to the nearest 0.1 g with Pesola scales or an ACCulab portable electronic balance (large snakes); date and 24-hour time (military); and activity. All snakes were scale-clipped. A small PIT-tag, read with an Avid tag reader, was inserted subcutaneously into the larger species.

Internal body temperature was recorded by means of cloacal temperature (BT) to 1°C with a Schultheis quick-reading thermometer. Corresponding air (AT), and surface (ST) or water temperatures (WT) were recorded to 1°C with a mercury thermometer. Also noted were the location; habitat; snake activity: basking (B), under cover (C), foraging/feeding (F), hibernating (H), moving (M, crawling on land, climbing, or swimming in water), and reproductive (R) (courting, mating, gravid female). All snakes were released at the point of capture. Snakes were considered active if they moved when touched. It was not always possible to take a snake's BT, as some escaped or were too small. Such events were recorded as observations, but the environmental temperatures (ETs) were recorded immediately after the observation at the snake's exact position.

RESULTS AND DISCUSSION

Annual Activity Period. North American snakes experience different seasonal periods of annual activity due to elevation and latitude, with peaks

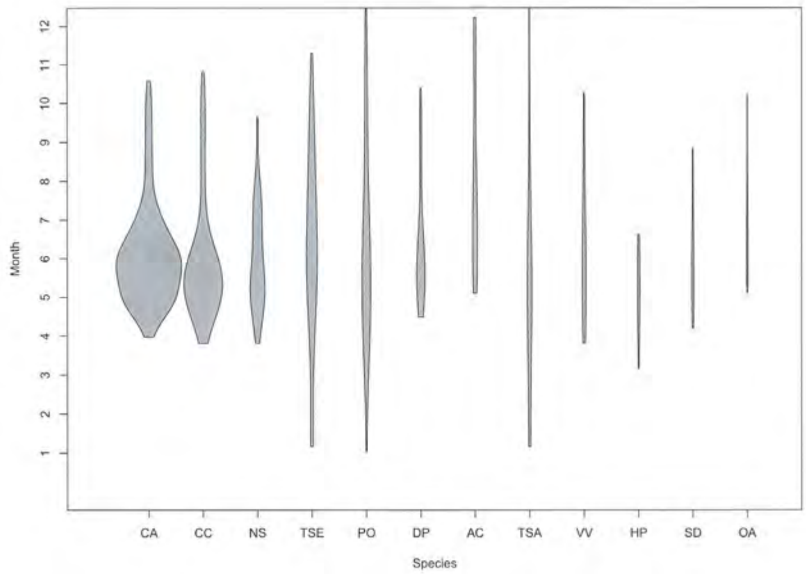

Figure 1. Annual snake activity by months (AC, *Agkistrodon contortrix*; CA, *Carphophis amoenus*; CC, *Coluber constrictor*; DP, *Diadophis punctatus*; HP, *Heterodon platirhinos*; OA, *Opheodrys aestivus*; PO, *Pantherophis obsoletus*; SD, *Storeria dekayi*; TSA, *Thamnophis sauritus*; TSE, *Thamnophis sirtalis*).

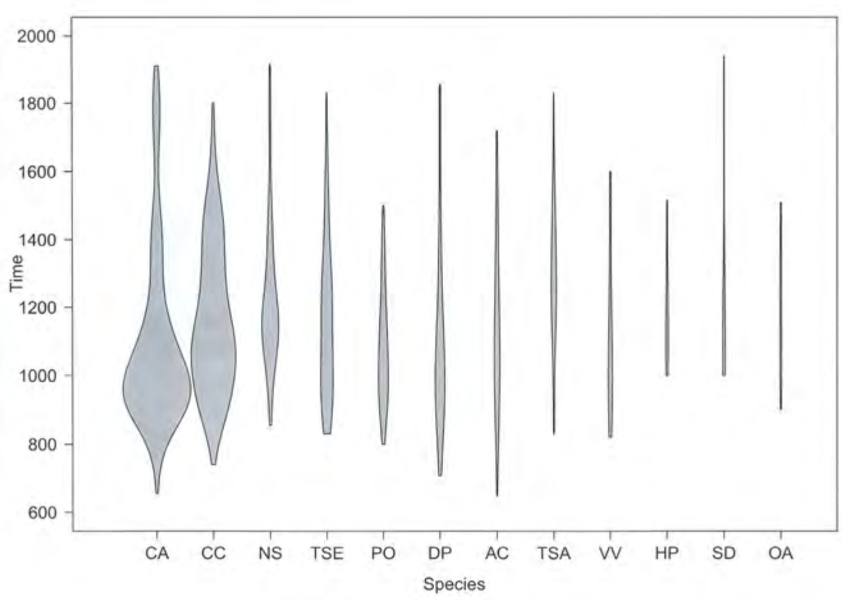

Figure 2. Daily snake activity by 24-hour (military) clock (AC, *Agkistrodon contortrix*; CA, *Carphophis amoenus*; CC, *Coluber constrictor*; DP, *Diadophis punctatus*; HP, *Heterodon platirhinos*; OA, *Opheodrys aestivus*; PO, *Pantherophis obsoletus*; SD, *Storeria dekayi*; TSA, *Thamnophis sauritus*; TSE, *Thamnophis sirtalis*).

of surface abundance occurring at different times of the year. Except in the more southern states, and especially in Florida, snakes are least surface active during the period December-February, with more northern species hibernating then (Ernst & Ernst, 2003). With the onset of spring, ETs rise, daylight increases, and snakes become correspondingly active.

Ectothermic snakes do have some control of BT selection through behaviour. A number of factors are involved in the maintenance of snakes' annual activity cycles: size (possibly age), attainment of maturity (adult, juvenile/immature, neonates), female and male hormonal cycles, prey availability, and microhabitat needs (Gibbons & Semlitsch, 2001; Ernst & Ernst, 2003).

Heterodon platirhinos was the only Mason Neck snake that exhibited a unimodal activity pattern (Figure 1); Platt (1969) reported a bimodal activity pattern in Kansas. At Mason Neck it was most often encountered in late spring and early summer during its mating season, and when its prey (toads, *Anaxyrus americanus* and *A. fowleri*; salamander, *Ambystoma maculatum*) were most available (Ernst and Laemmerzahl, 1989; Ernst & Ernst, 2003).

The other Mason Neck snakes with sufficient encounters had bimodal patterns, being active over the summer with a first peak beginning in late spring and continuing into early summer (associated with emergence from hibernation, basking, courtship/mating, and onset of feeding), diminished activity during the warmest summer months (July-August), and a second peak (involving some courtship/mating, but mostly parturition or hatching; diminished prey availability and cessation of feeding; and later movement to hibernacula) in late summer and early fall (mid-September through October). The earliest and latest dates of capture or observation are listed in Table 1; and the annual activity periods of some Mason Neck snakes are shown in Figure 1. Collectively, Mason Neck snakes were active from April through October, with a few outliers in March and November, and the two species of *Thamnophis* and *Agkistrodon contortrix* on warm days in December and early January. All species sought hibernacula in October, and by mid- to late-November all were only found at such sites. The majority of individuals did not arise again until April. Most annual activity occurred

Species (N)	**Earliest Date**	**Latest Date**
Carphophis amoenus (328)	March 30	October 18
Coluber constrictor (194)	March 25	October 25
Nerodia sipedon (73)	April 25	September 20
Thamnophis sirtalis (54)	January 5	November 9
Pantherophis obsoletus (43)	January 1	December 26
Diadophis punctatus (42)	April 15	October 12
Agkistrodon contortrix (25)	April 24	December 7
Thamnophis sauritus (23)	January 5	December 23
Virginiae valeriae (18)	March 25	October 20
Heterodon platirhinos (11)	March 5	June 19
Storeria dekayi (11)	April 6	August 26
Opheodrys aestivus (7)	May 3	October 7
Lampropeltis calligaster (6) (recent hatchlings)	August 16	-
Lampropeltis getula (2)	April 18	May 31
Regina septemvittata (2)	April 23	May 14
Lampropeltis triangulum (1)	March 15	-

Table 1. Earliest and latest dates on which active snakes were encountered.

Species (N)	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
Carphophis amoenus (328)	-	-	C	C, R	C, R	C, R	C, M	C	C, M,R	C	-	-
Coluber constrictor (194)	-	-	C, M,B	C, M, B, F, R	C, M, B, F, R	C, M, B, F	C, M, B, R	C, M, B, F	C, M	C, M, B	-	-
Nerodia sipedon (73)	-	-	B	C, M, B	M, B	M, B, F, R	M, B	M, B	F	-	-	-
Thamnophis sirtalis (54)	R	-	C	M, B, F	C, M, B	C, M, B,F, R	C, M, B	M, B	C, M	C, M, B, R	M	-
Pantherophis obsoletus (43)	H	-	H, M, B	C	C, M, B, F	C, M, B	C, M, B	C, M	C	H, C, M	H	H
Diadophis punctatus (42)	-	-	-	C	C, M	C, M	C	C	C	C	-	-
Agkistrodon contortrix (27)	-	-	-	R	C, M, B	C, B	C, B	C	C	C	B	B
Thamnophis sauritus (23)	B	-	-	M, B	M, B	M	-	B	M	-	-	B
Virginia valeriae (18)	-	-	C	C, M	C	C	C	C	C	C	-	-
Heterodon platirhinos (11)	-	-	C	C, F	C, M	M, B, F	-	-	-	-	-	-
Storeria dekayi (11)	-	-	-	C, M	C	C, B	-	C, M	-	-	-	-
Opheodrys aestivus (7)	-	-	-	-	M	M	-	-	-	M	-	-

Table 2. Snake behavior by months: B = basking, C = cover, F = forage/feeding, H = hibernaculum, M = move (crawl on land, climb, swim), R = reproductive (court, mate, gravid female).

during April-June, and noticeably slowed from July through September; most species were less surface active and under cover after June. This was particularly true of the smaller snakes (*Carphophis*, *Diadophis*, *Storeria*, *Virginia*); perhaps as daylight hours became too hot and dry, they shifted to a more crepuscular or nocturnal activity cycle. Such a time shift was also evident in the pitviper *A. contortrix*. Summer heat and drier conditions affected the larger *Coluber* and *Pantherophis* less, although there were fewer surface captures after June. Aquatic and semiaquatic snakes (*Nerodia*, *Thamnophis sauritus*, *T. sirtalis*) that could cool themselves in water, were also less active and usually found only in aquatic microhabitats after June. This annual cycle was expected, and fills an eastern mid-latitude data gap.

Some species' annual activity may have been at least partially controlled by their preys' cycles. *Coluber* and *Pantherophis* feed mostly on small mammals which are active throughout the year and their annual activity periods show this (Figure 1), while *Nerodia* and the two *Thamnophis* feed on fish, amphibians, small mammals (*T. sirtalis*), or earthworms throughout their annual activity period (Ernst & Ernst, 2003). Contrastingly, *Carphophis*, *Diadophis*, and *Storeria*, which feed predominately on earthworms (Ernst & Ernst, 2003; Orr, 2003, 2006) decreased in numbers after June, and possibly become more crepuscular or nocturnal to match the active times of earthworms.

Smaller individuals of each species became active later in the spring than did larger, more mature ones. The only small snakes found active in March were the single captured *Lampropeltis triangulum*, a juvenile on 15 March; an adult male Virginia on 25 March; and an adult male *Carphophis* on 30 March; all were under cover. Males also dominated in April, with females and smaller individuals becoming more active after the 15th. In contrast, captures from late September to mid-November were about even between the adult sexes and immatures.

Daily Activity Period. The daily activity cycle indicates the time of day in which the snakes' major surface activities occur (Gibbons & Semlitsch, 2001). Such patterns are usually determined by the time the best ranges of AT and ST are available for normal surface activity (including basking), times correlated with rainfall events, their prey activity cycles, the hours when the opposite sex is most active (during the mating season, or during the female's time of oviposition or paturition), and the time of appearance of neonates (Figure 2, Table 3).

Daily activity at Mason Neck was categorized as either diurnal (active during the daylight hours), crepuscular (active during the transition between day and night when days become warmer in late

Species (N)	0600	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900
Carphophis amoenus (188)	C	C	C	C, M, R	C, R	C	C	C	C	C	-	C, M, R	C	C
Coluber constrictor (156)	-	C	C, B	C, M, B, F, R	C, M, B, R	C, M, B, R	C, M, B, F	C, M, B, R	C, M, B, R	C, M, B, F	C, M, B	C, M	C	-
Nerodia sipedon (65)	-	C	C, M	B, R	M, B	M, B, F	M, B	M, B	M, B	-	B	M	B	-
Pantherophis obsoletus (39)	-	-	C, M	C, M, H	C, M, B	C, M, B, H	C, M, F	C, M, B	M, B	M	-	-	-	-
Thamnophis sirtalis (34)	-	-	B	C, M,B	C, M, B	C, M, F	M, B, R	M, B	M, B	C	C, B	-	M	-
Diadophis punctatus (31)	-	-	-	C, M	C	C	-	C, M	C	B	B	-	C, M	-
Thamnophis sauritus (23)	-	-	B	C	B	M	M, B, H	M	M, B, H	B	B	-	M	-
Agkistrodon contortrix (24)	M	-	C	C, B	C	C, B	B	B, R	C, M, B	-	C	-	-	-
Virginia valeriae (11)	-	-	C	C	C	C	-	C, M	-	-	C	-	-	-
Heterodon platirhinos (11)	-	-	-	C	C, M, F	C, M, F	B	B	-	F	-	-	-	-
Storeria dekayi (10)	-	-	-	-	C, M	C	B	-	-	-	-	C	-	M
Opheodrys aestivus (7)	-	-	M	M	M	-	M	M	M	-	-	-	-	-

Table 3. Daily snake behavior by 24-hour (military) clock: B = basking, C = cover, F = forage/feeding, H = hibernaculum, M = move (crawl on land, climb, swim), R = reproductive (court, mate, gravid female).

spring and summer and a reverse of this pattern in the autumn), or nocturnal (active after nightfall). Diurnal snakes included *Coluber*, *Heterodon*, *Nerodia*, *Pantherophis*, and *Thamnophis*. *Carphophis*, *Diadophis*, *Storeria*, *Virginia*, and *Agkistrodon* were crepuscular/nocturnal. This simplistic approach causes overlap in some species because of increasing or decreasing hourly AT and ST during the year. Diurnal surface activity at Mason Neck became earlier in the day as spring advanced and later with the progression of autumn. In summer, some species (*Agkistrodon*, *Carphophis*, *Nerodia*) became active earlier in the dawn hours, went under cover during the hottest mid-day period, and again became active during the late afternoon and dusk hours as AT fell.

Unfortunately, nocturnal research at the refuge was not permitted, and the refuge was locked as darkness approached. Therefore, we were dependent on previous literature reports of nocturnal activity in some species present (see Ernst & Ernst, 2003) and the fact that some species were almost exclusively found under cover during the daylight hours (*Carphophis*, *Diadophis*, *Storeria*, *Virginia*).

Annual and Daily Behaviour Cycles. Behaviour of Mason Neck snakes changes during its annual activity period (Table 2). The snakes' behaviour is most dependent on the ET with which it is most in contact (AT, ST, WT); but also by their reproductive hormonal cycles, and the most advantageous time to find prey (Ernst & Ernst, 2003); and once Spring ATs become warm enough to bring them to the surface, they first begin to bask for more body heat. Then, as AT and ST allow other surface activities, the snakes begin to move about and search for mates and prey. Most species oviposite in June.

Because of excessive daytime ETs in July and August, most snakes remain under cover during the warmest hours and are active in the early morning, late afternoon or evening when ETs do not stress them. A second, lesser period of reproductive activity occurs in September-October (Table 2). Late August-October is also the time when neonates first appear. Activity slows in the autumn as ETs fall with few snakes surface active after October, and all essentially in hibernacula in late November through February (Figure 1, Table 2).

Data in Table 3 indicate that courtship/mating activity may occur anytime during 0900-1700 hours when the two sexes meet, and the ETs are suitable. In the smaller, nocturnal *Carphophis* reproductive behaviour was only noted when the two sexes were found situated side by side or in close proximity under cover together; however, this does not preclude such nocturnal activity when the species is moving over the surface (Barbour et al., 1969).

As stated in the introductory remarks, this study provides valuable comparative information for possible future studies on the effects of climate change on reptiles in the Middle Atlantic states. Increased environmental temperatures may already by affecting the herpetofauna of the region. In the latter years of our research at Mason Neck, we have observed possible signs of this in the turtle *Kinosternon subrubrum*. A survey of many nesting records reported by Ernst and Lovich (2009) indicates that the turtle normally nests during late May and June, although scattered observations of nesting have been reported from farther south and west on 31 March (a single record; Richmond, 1945) to September. Prior to 2000, nesting at Mason Neck had only been observed in late May and June (Gotte, 1988). Since then we have found female *K. subrubrum* either excavating a nest cavity or ovipositing on four earlier dates: 30 March (ovipositing; Orr & Ernst, 2002), 15 April (excavating; Ernst et al., 2001), 24 April (excavating), and 1 May (ovipositing). If female Mason Neck *K. subrubrum* have been affected by warming climate change, so possibly have the refuges' snakes; thus making the data we present very important for future studies in this region of North America.

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