Characteristics of a snake community in northern Virginia, USA

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ABSTRACT - The population characteristics of a community consisting of 16 species of snakes occurring in five microhabitats were studied for 24 years (1982 to 2006) at the Mason Neck National Wildlife Refuge, Fairfax County, Virginia, USA. The portion of the refuge studied included five varied microhabitats: an old farmstead, and old field, extensive woodlands, a pond, and a tidal marsh. The species morphological characteristics, adult male/female ratios, and juvenile/adult ratios are reported, as also are the snake biomass, numbers, richness of each microhabitat and changes in the fauna over the time period. Niche characteristics of the snake species are described. Comparisons are made with Middle Atlantic snake communities to the north and south of Mason Neck.

INTRODUCTION

Reports of ecological studies of individual species of North American snakes are common (Ernst & Ernst, 2003, 2011). However, studies of the structure and dynamics of communities consisting of several North American snakes are more rare (Ernst & Ernst, 2003).

To our knowledge, the only such published studies involving diverse snake communities in the Middle Atlantic States have been those by Meshaka (2010), Meshaka & Delis (2014) and Meshaka et al. (2008, 2009) at sites to the north in central and western Pennsylvania and Mitchell (2014) at another more southern site in central Virginia.

The snake community at the Mason Neck refuge consisted of 16 species (Table 1): *Agkistrodon contortrix* (L.) [copperhead, N = 24 individuals]; *Carphophis amoenus* (Say) [eastern worm snake, N = 238], *Coluber constrictor* L. [racer, N = 204], *Diadophis punctatus* (L.) [ring-necked snake, N = 54], *Heterodon platirhinos* Latreille [eastern hog-nosed snake, N = 11], *Lampropeltis calligaster* (Harlan) [yellow-bellied kingsnake, N = 6], *L. getula* (L.) [common kingsnake, N = 3], *L. triangulum* (Lacépède) [milk snake, N = 1], *Nerodia sipedon* (L.) [northern water snake, N = 67], *Opheodrys aestivus* (L.) [rough green snake, N = 6], *Pantherophis alleghaniensis* (Holbrook) [rat snake, N = 43], *Regina septemvittata* (Say) [queen snake, N = 6], *Storeria dekayi* (Holbrook) [DeKay's brown snake, N = 12], *Thamnophis sauritus* (L.) [common ribbon snake, N = 26], *T. sirtalis* (L.) [common garter snake, N = 55], and *Virginia valeriae* Baird and Girard [smooth earth snake, N = 16].

Earlier research on Mason Neck snakes were by Creque (2001), Ernst et al., (2012, 2014), Hansknecht et al., (1999), Hartsell (1993), Klimkiewicz (1972), and Orr (2003, 2006); and formed the major emphases of the research. Although our studies there began as examinations of various aspects of the ecology of *Carphophis amoenus*, according to Gibbons (2013), regardless of the original intent of studies that last longer than planned, they often provide empirical data needed to address important biological questions.

The results of our long-term research on the populations and community structure and dynamics of this northern Virginia snake assemblage are presented below.

MATERIALS AND METHODS

Field-site description

Collections were made at a 30-ha site on an Atlantic Coastal Plain peninsula jutting into the Potomac River at the Mason Neck National Wildlife Refuge, Fairfax County, VA (38°67'N, 77°10'W; ≈25-35 m elevation). The site was restricted and closed to the general public, and its microhabitats were maintained during the study. The peninsula's vegetation is composed primarily of mixed deciduous upland forest. The length of the peninsula is bisected by a gravel road. The study area included five different microhabitats: (A), An old farmstead consisting of mixed hardwoods, grass plots and a parking area at the terminal point of the peninsula where cover boards were placed and the debris from the original farmhouse and outbuildings provided cover for snakes; (B), a >3-ha field undergoing succession with the transecting gravel road to the south and surrounded on the other three sides by woods; cover boards were placed along its borders to join several wood piles and abandoned railroad ties. (C), a ≈2-ha freshwater pond fed by a brook to the south, surrounded by woods on two sides, the gravel road to the north, and a brook flowing northward to a tidal marshland. (D), a ≈5-ha tidal-freshwater marsh along the Potomac River to the north, and (E), an extensive mixed second and third growth woods separating the other four microhabitats.

Field materials and methods

Snake collections occurred over 24 years from April 1982 through August 2006, but predominately from 1990 to 2006, and were conducted mostly during the prime annual snake-activity period at this site (April-November; Ernst et al., 2012). Nine aged wooden boards and 14 abandoned sheets of roofing tin were provided as "cover boards" to shelter snakes (Grant et al., 1992). Most data were derived from hand collections because the use of drift fences was prohibited by Refuge policy (additional captures of some rare and secretive snakes may have occurred if this method had been available; Durso et al., 2011). We routinely examined natural hiding places (downed logs and rocks) and manmade debris (old wood railroad ties, cinder blocks, sections of an old concrete sidewalk, and an old brick spring house).

Data collected from each snake at capture included the date, 24-hour military time, microhabitat, its behaviour (separately moving on land or in water, basking, foraging/feeding [ingesting], courting/mating, or undercover/hibernating); maturity stage (male, female, or juvenile/immature based on size at attainment of sexual maturity; Ernst & Ernst 2003); and total body length (TBL) and tail length (TL) measured with a cloth measuring tape (large snakes) or a standard metric ruler (small snakes). Snout-vent length (SVL) was calculated by subtracting TL from TBL. We recorded the mass of each snake to the nearest 0.1 g with Pesola spring scales. Snakes heavier than 1000-g were weighed with an ACCulab portable electronic balance of 4000-g capacity. Standard scale-clipping was used to mark all snakes for future identification (Brown & Parker, 1976). Larger species were marked with coded passive integrated transponder (PIT) tags inserted subdermally to track their movements. Recapture data from the same date were not recorded. After processing, snakes were released at the point of capture. Snakes were considered active if they responded (moved) when handled.

Data analysis

Data were gathered over a relatively long period at different diel times, dates, and meteorological conditions, and used to determine the snake community characteristics/relationships (see Ernst et al., 2012, 2014 for snake annual and diel activity cycles and thermal ecology at the site).

RESULTS AND DISCUSSION

Species structure and numbers

The community structure of the snakes at Mason Neck during our years of research consisted of 16 species; a diverse species assemblage for a rather northern site. The number of encounters, morphological characters, biomass, adult sex ratio, and juvenile/adult ratio of each species are presented in Table 1.

In a previous short-term reptile census conducted at Mason Neck, Klimkiewicz (1972) reported *P. alleghaniensis* and *T. sirtalis* as abundant; *C. amoenus*, *C. constrictor*, *N. sipedon*, and *S. dekayi* common; *A. contortrix*, *D. punctatus*, *H. platirhinos*, *L. calligaster*, *L. getula*, *O. aestivus*, *Storeria occipitomaculata* (red-bellied snake), *T. sauritus*, and *V. valeriae* uncommon; and *Farancia erytrogramma* (rainbow snake), *L. triangulum*, *Pantherophis guttatus* (red corn snake), and *R. septemvittata* hypothetically occurring at the site.

In contrast, based on data in Table 1, we consider *C. amoenus* and *C. constrictor* very abundant; *A. contortrix*, *D. punctatus*, *N. sipedon*, *P. alleghaniensis*, *T. sauritus*, *T. sirtalis* common; *H. platirhinos*, *O. aestivus*, *S. dekayi* and *V. valeriae* uncommon; *L. calligaster*, *L. getula* and *R. septemvittata* rare; and *L. triangulum* extremely rare at Mason Neck.

Neither *P. guttatus* nor *S. occipitomaculata* were found during our years of research, although both have been reported, respectively, from Prince William County and Fairfax County, Virginia (Ernst et al., 1997). It is extremely unlikely that *F. erytrogramma* occurs in northern Virginia (Mitchell, 1994).

More recently, on 22 May, 2010, several groups of collectors surveyed the herpetofauna of the Mason Neck Refuge and parts of the adjacent Mason Neck State Park. They recorded 60 *C. amoenus*, 20 *N. sipedon*, 11 *C. constrictor*, 8 *P. alleghaniensis*, 5 *D. punctatus*, 3 *T. sauritus*, 1 *R. septemvittata*, 1 *S. dekayi*, and 1 DOR *H. platirhinos* (Orr & Mendoza, 2011). All 9 species had been previously found by us. However, they did not report *A. contortrix* and *T. sirtalis*, which were common during our research; *O. aestivus* and *V. valeriae*, recorded by us as uncommon; and *L. calligaster* and *L. getula* we considered rare; and the extremely rare *L. triangulum*. That a single *R. septemvittata* was found is noteworthy as it had not been collected by us since the 1980s. Undoubtedly, more snake species would have been recorded if the more current survey had included additional days and our specific study microhabitats.

Biomass and snake density

Total snake biomass at Mason Neck was 228.677 kg. Total biomass of the snake species was calculated by adding the masses of all new individuals captured of that species; total snake biomass at the five microhabitats was calculated by adding the masses of all snakes captured there (Table 2). Although the most common snake, *C. amoenus*, accounted for the greatest number of individuals (238) and captures (551), because of its small size and weight, it contributed only 0.66% of the total snake biomass. Most biomass was contributed by the largest two species *C. constrictor* (32.0%) and *P. alleghaniensis* (56.0%). The other 13 species accounted for approximately 11.7% of the total biomass although they amounted to 37.2% of the total 772 individual snakes captured during the study. Both size and biomass of the individual species is obviously correlated with their prey preference and mode of capture (Table 3).

Table 1. Captures (N), morphological characteristics, mass, adult sex ratio; juvenile/adult ratio of snake species at the Mason Neck National Wildlife Refuge, Fairfax County, Virginia, 1982-2006. All measurements in mm, snout vent length (SVL), mass in grams (g), males (M), females (F), juveniles (J), venomous (*). See text for additional data on individual snake species.

Species (N)	SVL Mean (Range)			Mean Mass	M	F	J	Adult M/F Ratio	Juvenile/ Adult Ratio
	M	F	J						
C. amoenus (551)	201 (160-254)	219 (168-268)	131 (50-178)	4.7	152	106	62	1.43/1.00	0.24/1.00
C. constrictor (145)	871 (580-1170)	882 (540-1232)	296 (240-400)	397.4	68	62	15	1.10/1.0	0.12/1.00
N. sipedon (66)	590 (411-825)	694 (451-819)	360 (155-475)	189.1	31	20	15	1.55/1.00	0.29/1.00
T. sirtalis (57)	437 (385-495)	359 (280-430)	196 (45-222)	60.4	31	13	13	2.38/1.00	0.30/1.00
P. alleghaniensis (44)	861 (465-1430)	1148 (781-1810)	398 (210-490)	297.2	25	18	1	1.86/1.00	0.23/1.00
D. punctatus (43)	23 (18-32)	24 (19-35)	12 (9-14)	1.6	12	21	10	0.57/1.00	0.30/1.00
T. sauritus (27)	44 (39-50)	36 (29-43)	19 (15-22)	189.0	18	4	5	4.50/1.00	0.23/1.00
A. contortrix (23) *	65 (54-86)	71 (62-83)	31 (21-43)	205.1	7	10	6	0.70/1.00	0.35/1.00
V. valeriae (19)	141 (104-187)	211 (170-261)	114 (105-120)	5.4	6	5	8	1.2/1.00	0.73/1.00
H. platirhinos (12)	548 (457-716)	604 (480-718)	232 (230-233)	197.4	6	4	3	1.50/1.00	0.30/1.00
S. dekayi (12)	220 (180-270)	230 (190-270)	150 (140-180)	5.5	6	5	2	1.20/1.00	0.20/1.00
O. aestivus (8)	480 (370-590)	480 (450-540)	-	5.5	3	5	-	0.60/1.00	-
L. calligaster (6)	-	-	180 (170-190)	4.5	-	-	6	-	-
L. getula (3)	780 (700-850)	-	-	28.5	3	-	-	-	-
R. septemvittata (2)	390	340	-	100.3	1	1	-	1.00/1.00	-
L. triangulum (1)	-	-	180	7.0	-	-	1	-	-

Microhabitat use and species density

Occupancy of the five microhabitats (Table 2) at Mason Neck by the individual snake species varied; and was probably determined by the availability of the particular snake's diet preferences (Ernst & Ernst, 2003; Vitt, 2001), although the presence of cover and suitable environmental temperatures and humidity which retarded desiccation (Elick & Sealander, 1972) probably also played important roles.

The presence of five different microhabitats allowed a greater number of prey species. Twelve snakes (75% of total species) were captured at the farmstead (microhabitat A) and in the woods (E), 10 species (62.5%) at the mostly open old field (microhabitat B), but only four species (25.0%) were found at either the pond (C) or marshland (D). Snake biomass was greatest at the farmstead, old field and woodland microhabitats due to the greater presence of the two heaviest snakes, *Coluber* and *Pantherophis*.

Terrestrial *C. amoenus* were only found at the farmstead (A, 55.9% of its captures), under cover along the ecotonal borders of the old field (B, 15.4% of captures), and throughout the woodlands (E, 28.8% of captures). *C. constrictor*, usually terrestrial, occurred in four biohabitats: A, 38.0%, B 45.7%, D, the marsh, 0.5%, and E, 15.8%. It was the most heat tolerant of the snakes at the old field (Ernst et al., 2014); and often found crawling in the open at noon on very hot days; with the exception of *H. platirhinos* (one individual), the other snakes found at B were confined to the more shaded ecotonal borders of the field where more cover was available. The terrestrial/ arboreal *P. alleghaniensis*, was captured in all five microhabitats: A, 72.1%, B, 2.3%, E, 22.3%, and one each (2.3%) was surprisingly found swimming in the pond (C)

Table 2. Snake biomass and numbers for microhabitats at the Mason Neck National Wildlife Refuge, Fairfax County, Virginia, USA, 1982-2006. N = captures. * = venomous.

Species (N)	Old Farmstead (N)	Old Field (N)	Pond (N)	Woodland (N)	Marsh (N)	Total Species Biomass
C. amoenus (320)	0.840 kg (194)	0.232 kg (44)	-	0.433 kg (82)	-	1.505 kg
C. constrictor (145)	27.815 kg (70)	33.378 kg (45)	-	11.523 kg (29)	0.397kg (1)	73.113 kg
N. sipedon (66)	0.189 kg (1)	-	11.348 kg (60)	-	0.946 kg (5)	12.483 kg
T. sirtalis (57)	1.510 kg (25)	0.242 kg (4)	1.389 kg (23)	0.302 kg (5)	-	3.443 kg
P. alleghaniensis (44)	9.232 kg (31)	0.298 kg (1)	0.298 kg (1)	2.680 kg (10)	0.298 kg (1)	128.061 kg
D. punctatus (43)	0.154 kg (28)	0.044kg (8)	-	0.039 (7)	-	0.237 kg
T. sauritus (27)	-	0.018 kg (1)	0.467 kg (26)	-	-	0.485 kg
A. contortrix (23)*	3.500 kg (17)	-	-	1.235 kg (6)	-	4.735 kg
V.valeriae (19)	0.063 kg (12)	-	-	0.037 (7)	-	0.100 kg
H. platirhinos (12)	0.789 kg (4)	0.987 kg (5)	-	0.592 kg (3)	-	2.368 kg
S. dekayi (12)	0.548 kg (8)	0.006 kg (1)	-	0.018 kg (3)	-	0.572 kg
O. aestivus (8)	-	0.055 kg (1)	-	0.382 kg (7)	-	0.437 kg
L. calligaster (6)	-	-	-	0.045 kg (6)	-	0.045 kg
L. getula (3)	0.285 kg (1)	0.285 kg (1)	-	0.285 kg (1)	-	0.855 kg
R. septemvittata (2)	-	-	-	-	0.201 kg (2)	0.201 kg
L. triangulum (1)	0.007 kg (1)	-	-	-	-	0.007 kg
Total biomass	44.932 kg	35.545 kg	13.502 kg	17.571 kg	1.842 kg	228.677 kg
# species (captures)	12 (357)	10 (111)	4 (110)	12 (566)	4 (9)	16 (753)

and crawling in the marsh wetlands (D). *T. sirtalis* was found in microhabitats A (43.9%), B (7.0%), C (40.4%), and E (8.8%), but surprisingly not in the marsh (D). It is the most microhabitat generalist of the Mason Neck snakes, and does not require proximity to water (Carpenter, 1952); in contrast, *T. sauritus* was usually found in brush near water at the pond (C, 96.1%) and only once at the nearby old field (B, 3.8%). *D. punctatus* was captured only at the farmstead (A, 65.1%), ecotonal border of the old field (B, 18.6%) and in the woods (E, 16.3%; often behind the bark of trees). *V. valeriae* was found at the farmstead (A, 63.2%) and in the woods (E, 36.8%). Most of the aquatic *N. sipedon* were recorded at the pond (C, 90.9%) and marsh (D, 7.6%), although one (1.5%) was captured at the farmstead (A). Both *R. septemvittata* were collected in the marsh (D). The terrestrial/arboreal *O. aestivus* were, with one exception (old field B, 12.5%), confined to the woods (E, 85.5%). The venomous *A. contortrix*, was captured at the farmstead (A, 73.9%) and woods (E, 26.1%), where rodents were most abundant. The three species of *Lampropeltis* were rarely found: six hatchling *L. calligaster* under a log in microhabitat E, one adult *L. getula* each at A, B. and E, and a single juvenile *L. triangulum* at A. *Heterodon platirhinus* was found at the farmstead (A, 33.3%), old field (B, 41.7%), and woodland (E, 25.0%). S. dekayi were capture at the farmstead (A, 66.7%), woodland (E, 25%), and old field border (B, 8.3%). The abundance, richness and biomass per microhabitat of each Mason Neck snake species are presented in Table 2.

Niche partitioning

The breadth of the ecological niche of a snake allows it to occupy only particular microhabitats, and this leads to formation of particular species groups at specific microhabitats (Reinert, 1993). The niche characteristics of each Mason Neck snake are summarised in Table 3. As expected, the more aquatic species (*N. sipedon*, *R. septemvittata* and *T. sauritus*) were found predominately at the two most-moist microhabitats. The more generalist *T. sirtalis* was captured in all microhabitats, except, surprisingly, the marsh. The other more terrestrial species were found, with few exceptions at the old farmstead, woodland, and old field. The two arboreal species, *O. aestivus* and *P. alleghaniensis* occurred mostly at the old farmstead and woodlands where trees were common.

Presence of the primary prey (Ernst et al., 1997; Ernst & Ernst, 2003) played an important role in where the individual snake species foraged: *Agkistrodon, Coluber* and *Pantherophis* where rodents were common; and the worm-eaters *Carphophis*, *Diadophis*, *Storeria*, and *T. sirtalis* were found where this prey was most abundant. Amphibian predators such as *Nerodia* and the two species of *Thamnophis* were commonly found at the more wet microhabitats where frogs occurred. The other major amphibian predator, *H. platirhinos*, fed on toads (*Anaxyrus americanus* and *A. fowleri*) and spotted salamanders (*Ambystoma maculatum*; Ernst & Laemmerzahl, 1989), more terrestrial amphibians found predominately in the woodland or ecotone between the old field and adjacent woods.

Size and ontogeny of snakes are known to be correlated

Table 3. Niche characteristics of snakes at the Mason Neck Wildlife Refuge, Fairfax County, Virginia. *, data taken from Ernst and Ernst, 2003.

Species	Primary Foraging Habitat	Foraging Mode	Cycle Activity	Primary Prey	Primary Prey Detection	Capture Mode
C. amoenus	Terrestrial, Subterranean	Active Hunter	Nocturnal	Worms	Odor, sight (?)	Grab/swallow
C.constrictor	Terrestrial	Active Hunter	Diurnal	Small mammals (rodents, shrews) Lizards, small snakes, nesting birds	Sight, odor	Grab/swallow
N. sipedon	Aquatic	Active Hunter	Diurnal/ Crepuscular (anuran breeding season)	Fish, amphibians	Sight, odor	Grab/swallow
T. sirtalis	Terrestrial, Semiaquatic	Active Hunter	Diurnal/ Crepuscular (anuran breeding season)	Anurans, salamanders, worms, voles	Sight, odor	Grab/swallow
P. alleghaniensis	Terrestrial, Arboreal	Active Hunter	Diurnal	Small mammals (rodents, shrews, moles, chipmunks); squirrels (arboreal); birds; birds' eggs (arboreal)	Sight, odor	Constrict, Grab/ swallow
D. punctatus	Terrestrial	Active Hunter	Nocturnal	Salamanders, small anurans, insects, worms	Odor, sight	Grab/swallow (Envenomation)
T. sauritus	Terrestrial, Semiaquatic	Active Hunter	Diurnal/ Crepuscular (anuran breeding season)	Small anurans, salamanders, worms	Sight, odor	Grab/swallow
A. contortrix	Terrestrial	Ambusher, Active Hunter	Nocturnal/ Crepuscular, Seasonally Diurnal	Small mammals (rodents, shrews), ground nesting birds, insects (seasonal)	Body heat, sight, odor	Envenomation, Grab/swallow
V. valeriae	Terrestrial	Active Hunter	Nocturnal	Worms, slugs, insect larvae	Odor, sight	Grab/swallow
H. platirhinos	Terrestrial	Active Hunter	Diurnal	Toads, Ambystomid salamanders	Sight, odor	Grab/swallow (Envenomation?)
S. dekayi	Terrestrial	Active Hunter	Nocturnal/ Crepuscular	Worms, slugs	Odor, sight	Grab/swallow
O. aestivus	Arboreal, Terrestrial	Active Hunter	Nocturnal/ Crepuscular, Semidiurnal terrestrial	Insects, millipedes, isopods, snails*	Sight, odor	Grab/swallow
L. calligaster (juveniles)	Terrestrial	Active Hunter, Ambush (?)	Nocturnal	Insects; small salamanders, snakes and lizards, newborn mice/shrews*	Sight, odor	Constrict, Grab/ swallow
L. getula	Terrestrial	Active Hunter, Ambush (?)	Diurnal/Nocturnal (?)	Snakes, lizards, small mammals (rodents, shrews)	Sight, odor	Constrict, Grab/ swallow
R. septemvittata	Aquatic, Semiaquatic	Active Hunter	Diurnal (?)	Crayfish	Sight, odor	Grab/swallow
L. triangulum (juvenile)	Terrestrial	Active Hunter, Ambush (?)	Diurnal/ Nocturnal (?)	Young mice, shrews, salamanders, insects*	Sight, odor	Constrict, Grab/ swallow

with the size of their major prey (Arnold, 1993; Ernst & Ernst, 2003), and this was true at Mason Neck. With the exception of juveniles: adult snakes with invertebrate primary prey were the smallest (*Carphophis*, *Diadophis*, *Opheodrys*, *Storeria*, *Thamnophis*, *Virginia*); those that fed chiefly on amphibians tended to have medium lengths.

Prey preferences were the major factor differentiating the niches of the two *Thamnophis*, which were separated by the size of the amphibian species on which they predominately preyed (Carpenter, 1952). At Mason Neck, the larger *T. sirtalis* preys on larger ones (anurans: *A. americanus*, *A. fowleri*; *Lithobates catesbeianus* [larvae and recently transformed], *L. clamitans*, *L. palustris*, *L. sphenocephalus*, *L. sylvaticus*; salamanders: *A. maculatum*, *Plethodon cinereus*; but also some small snakes, lizards, and rodents). The shorter, more slender, *T. sauritus* preys on smaller animals (anurans: *Acris crepitans*; Hyla *chrysoselis-versicolor* complex, *H. cinerea*; *Pseudacris crucifer*, *P. feriarum*; salamanders: *Desmognathus fuscus*, *Eurycea bislineata*, *Hemidactylium scutatum*, and a few insects). Both species readily consume available earthworms.

Local rodent and bird predators were the largest snakes (*Coluber*, *L. getula*, *Pantherophis*). The largest prey we observed were a grey squirrel (*Sciurus carolinensis*) and eastern chipmunks (*Tamias striatus*) by both *Coluber* and *Pantherophis*. The two more arboreal snakes partitioned the tree niche by prey size (*Opheodrys*, insects and small invertebrates; *Pantherophis*, rodents, birds and their eggs).

The annual and daily activity patterns and thermal ecology of Mason Neck's snakes have been previously reported by Ernst et al. (2012, 2014). *Carphophis*, *Diadophis*, *Storeria* and *Virginia* have abbreviated annual cycles due to their more narrow range of operating body temperatures, and become scarce during the hot/dry months of the year, probably because of the greater possibility of desiccation and the scarcity of surface earthworms. The other species were generally active, with few exceptions, from late March/early April to October/early November.

Most captures of all species occurred during 0800-1600 hours. 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 by some species present (see Ernst & Ernst, 2003), and the fact that *Carphophis*, *Diadophis*, *Storeria* and *Virginia* were almost exclusively found under cover during the daylight hours. *A. contortrix* is nocturnal/crepuscular (Ernst & Ernst, 2003), and most were found under cover during the daylight hours, but some were active and captured as late as sunrise. Prey daily cycles probably influenced the foraging time of Mason Neck's snakes. Prey activity cycles also played an important role in setting both snake seasonal and diurnal activity cycles. Mason Neck *Heterodon* had an annual cycle strictly correlated with that of its amphibian prey.

The microhabitat and diet preferences, and both diel and annual activity cycles of Mason Neck *A. contortrix*, *C. amoenus*, *C. constrictor*, *D. punctatus*, *P. alleghaniensis*, *N. sipedon*, and *S. dekayi* closely match those of their Kansas congeners reported by Fitch (1982).

Capture data assembled during our 24 year study indicates that the Mason Neck's snakes have evolved their microhabitat preferences (Table 2) by adapting their foraging strategies and times to those of their primary prey (Table 3) and to the daily and annual cycles of these prey animals (Ernst et al., 2012).

Comparisons with other Middle Atlantic snake communities

Few studies of Middle Atlantic snake communities have been reported, and the microhabitats at these localities are different; making direct comparisons to Mason Neck difficult. In addition, these were conducted over shorter durations at piedmont or mountain localities composed of different microhabitats of varied dimensions and vegetation, had different species diversity, and used different collection methods than at Mason Neck (see the papers for details).

Two Pennsylvania studies north of Mason Neck (Meshaka, 2010; Meshaka et al., 2009) concentrated on snakes in Pennsylvania grasslands, and a third to the south (Mitchell, 2014) had about equal concentration in both fields and hardwood forest in the piedmont of Cumberland County, Virginia.

The 2010 study by Meshaka occurred in fields and mixed forest in the mountains of Westmoreland County. Those of Meshaka et al. (2008, 2009) were in piedmont grasslands in Dauphin and Lebanon counties. The Westmoreland study (Meshaka, 2010) included several different species than occur at Mason Neck, making it hard to compare the two sites; so only the snakes collected in its grassland microhabitat will be compared. *T. sirtalis* (756), *S. occipitomaculata* (123) and *D. punctatus* (88) dominated, with *L. triangulum*, *O. vernalis*, *N. sipedon*, and *C. horridus* also collected. At the two Pennsylvania piedmont sites, *T. sirtalis*, *C. constrictor*, and *P. alleghaniensis* dominated, with a few *D. punctatus*, *H. platirhinos*, *N. sipedon*, and *S. dekayi* present. Only 19 snakes were collected in the Virginia grassland by Mitchell (2014): *C. amoenus* (10), *S. occipitomaculata* (5), *S. dekayi* (4); but Mitchell thought his capture method provided an incomplete estimate of larger species (possibly *Coluber*, *Pantherophis* were missed).

Snakes captured, mostly in the ecotonal border, of Mason Neck's coastal plain field were *Carphophis* (44), *Diadophis* (8), *Heterodon* (4), *S. dekayi* (1), and *T. sauritus* (1). *Coluber* (45) was the most common snake in the open field; but *T. sirtalis* (4) and *Heterodon*, *L. getula*, *O. aestivus* and *Pantherophis* were each caught once (Table 2). *L. getula* and *O. aestivus* are rare in Pennsylvania and have been only reported from the most southeastern counties; and *Carphophis* is only known from the more mountainous and eastern regions of the Commonwealth (Hulse et al., 2001); otherwise the species reported from piedmont Pennsylvania sites are similar residents.

The most comparable study to Mason Neck was that of Meshaka & Delis (2014) at a Franklin County, Pennsylvania locality containing 12 natural or disturbed sites in wetlands, forest, thickets and open field microhabitats. Eight species were recorded, with 2-6 at each microhabitat. The three field habitats yielded six species: *Coluber* (28 individuals), *L. triangulum* (6), *Diadophis* (5), *Agkistrodon* (3), *T. sirtalis* (3), and *Pantherophis* (1). *Coluber* (5), *T. sirtalis* (2), and *L. triangulum* (1) were found in a thicket microhabitat. Three forest sites yielded *Diadophis* (23), *T. sirtalis* (29), *Coluber* (10), *L. triangulum* (5), and *Pantherophis* (2). *T. sirtalis* (38) and *N. sipedon* (16) dominated at two pond sites.

The greater species diversity at Mason Neck's microhabitats (Table 2) reflects our use of differentiated capture techniques and a much longer study. *Carphophis* was the most common snake at both of Mitchell's (2014) microhabitats. This was also true in our woodlands, but

Coluber (not captured by Mitchell) was equally common as *Carphophis* in our field ecotone. Its relative abundance at microhabitats of both studies probably reflects the presence of its major earthworm prey. This may also be true of *S. dekayi* in Mitchell's study. It is surprising that only one *T. sirtalis* was captured by Mitchell, as we found it more generalist in both habitat and diet preference (Tables 2 and 3). In fact, it was the most ubiquitous snake occurring at microhabitats of the Middle Atlantic community studies. Comparison of Meshaka & Delis (2014) and our study indicates that the more diverse the microhabitats at a site, the greater the snake diversity that can be supported.

The Mason Neck snake community through time

A summary of captures of individuals of each snake species between 1982 and 2006 is presented in Table 4. It gives the impression that some species increased in numbers over the period, while others declined. However, there were significant differences in total collections during the three decades which make statistical comparisons difficult and probably invalid.

Snakes were collected on 527 days from 1982-2006, and snakes were found on all days. During the 1980s (89 days, 16.9%), only Ernst was actively researching at Mason Neck, with only very occasional help from a few graduate students. His research then concentrated on the ecology of the turtle, *Terrapene carolina*, and snakes were only secondarily collected as encountered. During the 1990s (185 days, 35.1%), serious snake study began by Ernst and three graduate students (Hartsell, 1993; Creque, 2001; Orr, 2003, 2006). During this decade field trips (including up to 18 students from Ernst's Vertebrate Biology and Herpetology courses at George Mason University) were also taken to Mason Neck. Exact records of how many students and the duration of their collecting each trip were not recorded. However, the great increase in snakes captured then indicates more intense collecting, and is more indicative of the total numbers of both species and their populations present. Study from 2000-2006 (253 trips, 48%) was conducted by Ernst, Creque and Orr, and was the most intense study period. Unfortunately, daily time durations were not recorded. The lack of records of how many persons and the total time spent each trip make exact calculations of changes in snake populations impossible to determine; although generalities can be drawn.

More serious study during the 1990-2006 revealed more individuals of almost all species, and added *L. getula*, *L. triangulum* and *V. valeriae*. The two species not detected from the 1980s were *L. calligaster* and *R. septemvittata*. The six captured *L. calligaster* were recently hatched among their egg shells under a log in deep woodland; indicating reproduction was occurring at Mason Neck, although adults have not been collected. Due to its nocturnal and secretive habits (Ernst & Ernst, 2003), that this snake has not been detected since the 1980s does not mean that it has disappeared from Mason Neck. However, *R. septemvittata* may have had a reduction in numbers since the 1980s. This was a period of "acid rain" in Virginia, which had an adverse effect on the crayfish prey of the snake. But, one was found by Orr & Mendoza (2014), so a few probably still exist at the site.

Table 4. Comparison of numbers (N) of individuals captured in each decade of study of 16 species at the Mason Neck National Wildlife Refuge. * = decades of most concentrated study (see text).

Species (N)	1982-1989	1990-1999*	2000-2006*
C. amoenus (551)	105	223	223
C. constrictor (145)	19	75	51
N. sipedon (66)	4	37	25
T. sirtalis (57)	8	22	27
P. alleghaniensis (44)	5	31	8
D. punctatus (43)	3	17	23
T. sauritus (27)	4	15	8
A. contortrix (23)*	8	8	7
V. valeriae (19)	-	5	14
H. platirhinos (12)	4	6	2
S. dekayi (12)	4	3	5
O. aestivus (8)	3	5	-
L. calligaster (6)	6	-	-
L. getula (3)	-	3	-
R. septemvittata (2)	2	-	-
L. triangulum (1)	-	1	-
Total Captures (1019)	**175**	**451**	**393**
Total Species (16)	**13**	**14**	**11**

Several snakes were not captured during the 2000's, and this can be attributed to their relative scarcity (*Regina*, the three species of *Lampropeltis*) and the abbreviated collecting period. *O. aestivus* was also not captured by us or by Orr & Mendoza (2014), and may have actually declined. The snake is principally arboreal (Ernst & Ernst, 2003) and may have been missed; but another factor may have negatively affected its numbers. Northern Virginia trees experienced increased destruction by invasive Gypsy moths (*Lymantria dispar*) during the 1980s and early 1990s. Two attempts at reducing the moth population were made at Mason Neck. In 1989, the predatory wasp, *Meteorus pulchricornis*, was released, and during 1991-1995 a pesticide containing the microbe *Bacillus thuringiensis* was aerially sprayed over the refuge. These treatments may have drastically reduced the invertebrate prey of Opheodrys. Although we have no direct proof of this, three commonly found lizards (*Plestiodon fasciatus*, *P. laticeps*, *Scincella lateralis*) and the tree frog (*Hyla cinerea*), all insect predators and previously plentiful at Mason Neck, were reduced to only a few observable individuals during this period. Although anecdotal, this is an indication of the possible effect of such treatments on reptiles whose insect prey has been reduced.

CONCLUSIONS

Mason Neck still maintains a rich, diverse snake fauna due to its five different microhabitats (Table 2) which make available different prey species and ecological niches (Table 3). Such localities containing varied microhabitats are still plentiful in the Middle Atlantic Region; but, if they are to remain available in the future to support rich snake communities, they must be preserved.

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