Transactions of the Illinois State Academy of Science
(2015) Volume 108, pp. 39-42

received 5/25/15
accepted 6/20/15

Frequent Arboreal Behavior by Cottonmouths (*Agkistrodon piscivorus*)

John G. Palis
Palis Environmental Consulting, P.O. Box 387, Jonesboro, Illinois 62952, jpalis@yahoo.com

ABSTRACT

Cottonmouths (*Agkistrodon piscivorus*) are relatively wide-ranging, North American semi-aquatic pit vipers that frequent edges of water bodies. Although numerous literature accounts describe cottonmouths basking in trees and shrubs at the water's edge, a recent quantitative study in Alabama and Georgia suggests that arboreal behavior by cottonmouths is actually very rare (0.25% of 804 observations). In contrast, I observed frequent arboreal behavior by cottonmouths (42% of 1534 observations) during spring and fall at a southern Illinois wetland. Arboreal basking was particularly frequent in spring (57% of 1049 observations). Frequency of arboreal behavior did not differ between adult and juvenile cottonmouths, but juveniles perched higher than adults. My observations indicate that cottonmouths may frequently be arboreal, at least near the northern limit of their geographic range. Arboreal behavior might facilitate thermoregulation and/or predator avoidance.

Key words: *Agkistrodon piscivorus*, cottonmouth, arboreal behavior, basking, climbing, hibernacula, Illinois

INTRODUCTION

Snakes are ectothermic and use a variety of behavioral mechanisms to achieve and maintain preferred body temperatures (Avery, 1982; Lillywhite, 2014). Basking is chief among methods used by snakes to raise body temperature above ambient temperature (Avery, 1982; Peterson et al., 1993). The ability to raise body temperature above ambient temperature is especially important to populations occurring at higher latitudes or elevations where the active season is relatively short. Basking is particularly frequent in spring when snakes emerge from hibernacula (Gregory, 1982, 1984).

Cottonmouths (*Agkistrodon piscivorus*) are semi-aquatic vipers that range across the south-central United States from Texas to Florida northward through the Atlantic coastal plain to southern Virginia and through the Mississippi River drainage to Illinois and Missouri (Ernst and Ernst, 2003). Cottonmouths inhabit a variety of aquatic habitats ranging from brackish coastal marshes to freshwater streams, swamps, marshes, ponds, and lakes. Cottonmouths generally occur at the land-water interface (Gloyd and Conant, 1990; Ernst and Ernst, 2003), but can also be found considerable distances from water (Gloyd and Conant, 1990).

Near their northern range limit in southern Illinois (37° 41' N), large numbers of cottonmouths overwinter communally in rocky hillsides and bluffs (Cagle, 1942; Rossman, 1960; Palis, 2010). Cottonmouths emerge from hibernacula during the onset of warm weather in March and April, and return in September and October (personal observation). During fall ingress and spring egress, cottonmouths bask overtly upon the ground and rocks or amid leaf litter (personal observation). Cottonmouths sometimes bask above the ground or water in vegetation, especially during cool weather (Allen and Swindell, 1948; Blem and Blem, 1995; Gibbons and Dorcas, 2005). Quantitative data on the frequency of arboreal basking, however, is limited (Graham, 2013).

In 2010, I observed cottonmouths at a wetland-upland interface where, during spring and fall, large numbers of cottonmouths pass between active- and inactive-season habitats. Walking along the edge of the wetland during spring and fall, 2011–2014, I quantified frequency of substrate use by cottonmouths. Here, I compare frequency of cottonmouth use of four different substrates between spring and fall, placing a special emphasis on arboreal behavior to facilitate comparison of my observations with those of Graham (2013).

MATERIALS AND METHODS

I observed cottonmouths within Shawnee National Forest, Union County, Illinois. Weather records from the nearest weather station in Cape Girardeau, Missouri (approximately 14 km from study site) indicate that the region receives 119 cm of precipitation annually, and monthly mean air temperatures range from 0.6 C in January to 25.9 C in July. The study area encompasses the juncture of a west-facing, rocky-soiled, forested hillside characterized by a canopy of oaks (*Quercus* spp.), hickories (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), and tulip poplar (*Liriodendron tulipifera*), and a shallow-water, treeless wetland dominated by buttonbush (*Cephalanthus occidentalis*) and spadderdock (*Nuphar advena*). The east edge of the wetland is flanked by trees (principally silver maple [*Acer saccharinum*], river birch [*Betula nigra*], and sycamore [*Platanus occidentalis*]) and vines (peppervine [*Ampelopsis arborea*], trumpet creeper [*Campsis radicans*], catbrier [*Smilax bona-nox*], bristly greenbrier [*Smilax tamnoides*], winter grape [*Vitis cinerea*] and catbird grape [*Vitis palmata*]). Cottonmouths hibernate within the hillside and spend the summer in this and other nearby wetlands (personal observation).

I observed cottonmouths diurnally (median start time = 1230h) in spring (N = 8 surveys) and fall (N = 11 surveys) from 2011–2014. I surveyed from 20 March through 12 April (median = 6 April) in spring, depending upon the arrival of weather suitable for snake emergence from over-wintering, and from 30 August through 30 October (median = 25 September) in fall as snakes returned to the hillside. I observed cottonmouths as I walked slowly (mean survey time = 4.12 ± 0.71 hr) northward on a 1.9-km length of dirt trail that parallels the east bank of the wetland, at the base of the hillside.

I stopped frequently and visually scanned the trail and ground adjacent to the trail, the wetland bank and bank vegetation, and the wetland and wetland vegetation for the presence of cottonmouths. I used binoculars (10 x 40) to facilitate locating and identifying snakes at a distance. I tallied each cottonmouth observed, noted the substrate it was using and, for a subset of arboreal individuals (N = 419), visually estimated (± 25 cm) the height of individuals on perches above the water or soil. The height of individuals < 25 cm above water or ground was estimated ± 5 cm. I also categorized each individual as an "adult" or "juvenile" based on relative size, presence or absence of a yellow tail tip (presence indicated a yearling juvenile), and ontogenetic color pattern variation (dorsum of juveniles is boldly cross-banded, dorsum of adults is nearly uniformly black; Smith, 1961). I recorded air temperature (± 0.5 C) in shade 1 m above the ground 2–5 times per survey.

Following Graham (2013), I categorized snake locations as: (1) arboreal (snake occurring above the ground or water on a perch narrower than the snake, such as vines or narrow shrub or tree branches), (2) elevated (snake on log or other raised substrate above the ground or water that is wider than the snake), (3) terrestrial (snake on the ground, in a hole in ground, or in hole in base of tree), and (4) aquatic (snake in water). I did not capture or mark snakes; therefore, some individuals may have been observed more than once within and among years during the 4-yr survey. I attempted to reduce the likelihood of repeated within-season observations of the same individual by 1) separating surveys by an average of five days (2–11 d) in spring and 14 days (8–26 d) in fall, and 2) limiting my snake tally to those observed while I walked in one direction. Because I observed snakes in transient habitat, individuals observed within one season likely relocated by the next survey. Indeed, snake locations and numbers of snakes at specific locations frequently changed the same day. For example, on my post-survey walk southward, I frequently observed snakes at locations, or in numbers at specific locations, that differed from those observed during my northward survey. For all analyses, I treat each snake as an independent observation.

I compared frequency of cottonmouths in different locations between spring and fall surveys using a chi-square contingency table, and frequency of arboreal behavior of adult and juvenile snakes using a chi-square test. I used t-tests to make pair-wise comparisons of means of spring and fall air temperatures and wind speeds, heights of arboreal snakes in spring and fall, and heights of arboreal adults and arboreal juveniles. All means are presented as ± 1 SD and P <0.05 is considered statistically significant.

RESULTS

I categorized 1534 observations of cottonmouths during 19 surveys from 2011–2014. A total of 644 (42.0%) observations were of individuals on arboreal perches (Figure 1), 403 (26.3%) observations were of snakes on elevated substrates, 456 (29.7%) observations were of snakes on the ground, and 31 (2.0%) observations were of individuals in water. Cottonmouths were observed on arboreal substrates most frequently in spring (X^2 = 11.5, P = 0.001) and on terrestrial substrates more often in fall (X^2 = 22.7, P < 0.001; Figure 2). The frequency of cottonmouth observations on elevated substrates or in water did not differ between spring and fall (X^2 = 0.81, P = 0.37 and X^2 = 0.32, P = 0.57, respectively; Figure 2).

Although juvenile snakes (46.4%) and adult snakes (41.1%) were

Figure 1. Adult *Agkistrodon piscivorus* coiled in vines 0.75 m above the ground at the edge of a southern Illinois wetland in April 2014.

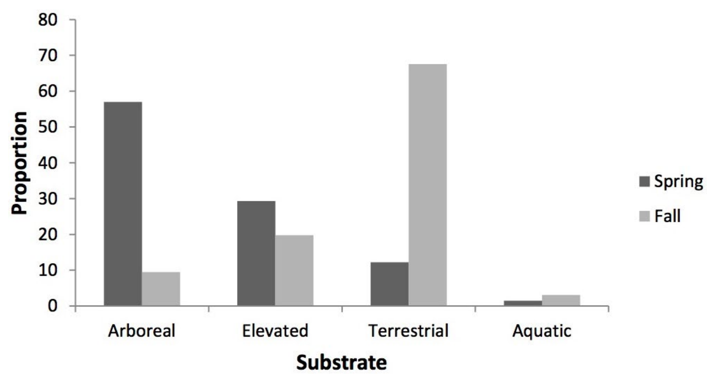

Figure 2. Proportion of 1534 *Agkistrodon piscivorus* observed on four substrate types during spring and fall.

equally arboreal (X^2 = 0.43, P = 0.52), juveniles perched higher (mean height = 107 ± 75 cm) than adults (mean height = 84 ± 65 cm; t = -3.26, df = 417, P = 0.001). Maximum estimated height above ground or water for both arboreal adults and juveniles was 450 cm (one observation of each). Height of arboreal adult snakes did not differ between spring (85 ± 67 cm) and fall (65 ± 42 cm; t=1.28, df = 275, P = 0.2), nor did height of arboreal juvenile snakes (spring: 105 ± 72 cm; fall: 116 ± 93 cm; = -0.58, df = 140, P = 0.56). Mean air temperature did not differ between spring (24.8 ± 2.3 C) and fall surveys(24.0 ± 2.6 C; t = 1.04, df = 58, P = 0.30), but wind speeds were greater during spring surveys (mean = 32.3 ± 9.0 km/hr) than fall surveys (mean = 14.8 ± 6.9 km/hr; t = 10.2, df = 83, P < 0.001).

DISCUSSION

The biology of ectotherms is strongly influenced by temperature, and latitudinal and altitudinal variation in temperature can exert a significant influence on behavior of individuals from different populations (Adolph, 1990; Weatherhead et al., 2012). For example, populations of ectotherms at higher elevations or latitudes have shorter annual activity periods than populations at lower elevations or latitudes (Sears, 2005; Weatherhead et al., 2012). Reduced activity periods might reduce time for energy acquisition and growth (Dunham et al., 1989; Beaupre, 1995). Ectotherms at higher elevations and latitudes overcome temperature restrictions by raising body temperature using behavioral means such as basking (Adolph, 1990; Weatherhead et al., 2012). Upon emergence in spring, temperate-zone snakes bask at or near hibernacula before dispersal to summer habitat (Prior and Weatherhead, 1996; Olsson et al., 1997; Row and Blouin-Demers, 2006). Near their northern range limit, cottonmouths are no exception, basking terrestrially on soil, rocks, and leaf litter before dispersal (personal observation). But why do cottonmouths frequently perch in vegetation at my study site? I offer a few potential, non-exclusive explanations.

Arboreal behavior by cottonmouths, particularly upon spring emergence from hibernacula, might provide greater thermoregulatory benefits than is available at ground level. In early spring, soil moisture is at its annual highest (Hollinger and Isard, 1994) and soil temperature is near its annual lowest (Changnon et al., 2004). Cottonmouths may attain and maintain preferred body temperatures more efficiently by getting above cold, damp ground into shoreline vegetation. In addition, water temperature in early spring is near its annual lowest (Harmeson and Schnepper, 1965). At the initiation of the two spring 2014 surveys, water temperatures in the wetland were 14.5 C and 18 C; 7.5 C and 6.0 C lower, respectively, than air temperature at the initiation of these surveys. Air temperatures were within, but water temperatures were below, the preferred body temperature of cottonmouths (mean = 23.4 C, range = 20.0–26.5 C; Crane and Greene 2008). Cottonmouths may climb shoreline vegetation before entering water, or climb into buttonbush after entering water, to gain access to their preferred temperature range (Tiebout and Cary, 1987; Roberston and Weatherhead, 1992; Weatherhead and Robertson, 1992). Because colder snakes swim more slowly than warmer snakes (Stevenson et al., 1985; Weatherhead and Robertson, 1992; Finkler and Claussen, 1999), raising body temperature before entering, or while crossing, the wetland may facilitate cottonmouth dispersal across cold water (Nelson and Gregory, 2000; MacKinnon et al., 2005).

Wind might also play a role in stimulating cottonmouths to climb into vegetation. During spring, weather fronts arriving from the south and southwest bring relatively warm air to southern Illinois. Although air temperature during spring surveys did not differ from fall surveys, wind speeds were greater during spring surveys and gusts during spring surveys were as high as 77.28 km/hr. Cottonmouths frequently swayed in the wind along with the small vines and branches upon which they lay. Because wind speed is greater above the ground than at ground level (Geiger, 1965) and increasing wind speeds bring body temperature of ectotherms closer to air temperature (Stevenson, 1985), cottonmouths might have climbed into vegetation to gain access to warm, southerly, spring winds. Further, narrower substrates, such as small-diameter branches and vines, may expose a greater proportion of each snake to air movement than larger-diameter elevated substrates.

Climbing into woody vegetation may also afford cottonmouths some protection from predation, particularly smaller individuals. Predators observed on site that are known to eat snakes include reptiles (snapping turtle [*Chelydra serpentina*], and racer [*Coluber constrictor*]), birds (great blue heron [*Ardea herodias*], red-shouldered hawk [*Buteo lineatus*], red-tailed hawk [*Buteo jamaicensis*], great egret [*Casmerodius albus*], and bald eagle [*Haliaeetus leucocephalus*]), and mammals (river otter [*Lutra canadensis*] and raccoon [*Procyon lotor*]; Allen & Swindell 1948, Gloyd and Conant 1990, Terres, 1991). Snakes in vegetation, whether above water or ground, may be less detectable by predators. In addition, attempts to extract cottonmouths intertwined with vegetation might put predators at risk of being envenomated. Smaller cottonmouths might climb higher than adults to avoid cannibalism.

Cottonmouths under my observation behave similarly to watersnakes. For example, Tiebout and Cary (1987) observed northern watersnakes (Nerodia sipedon) basking out of water in vegetation most frequently in spring, and Graham (2013) observed a spring bias in arboreal behavior by plainbelly watersnakes (*Nerodia erythrogaster*), northern watersnakes, and brown watersnakes (*Nerodia taxispilota*). In my study area, plainbelly watersnakes were also more arboreal in spring (46%) than fall (17%; $X^2 = 13.3$, df = 1, $P < 0.001$).

My observations of arboreal behavior by cottonmouths appear to support previous accounts (Garman, 1892; Allen and Swindell, 1948; Dundee and Rossman, 1989; Gloyd and Conant, 1990; Blem & Blem, 1995; Ernst and Ernst, 2003; Gibbons and Dorcas, 2005), but is at odds with observations made by Lillywhite and McCleary (2008) in Florida and with quantitative observations made by Graham (2013) in Alabama and Georgia. Inherent geographic variation in cottonmouth behavior may account for these differences. In addition, timing of Graham's investigations and my own may partially explain differences in our observations.

Graham (2013) initiated observations in March in Georgia and in April in Alabama. Average monthly air temperatures near Graham's study sites (Auburn Agronomy Farm, Alabama and Jonesboro, Georgia) are approximately one month ahead of southern Illinois (www.ncdc.noaa.gov). Therefore, cottonmouths observed by Graham (2013) in March and April may have emerged from hibernation a month or more before he initiated surveys. If greater arboreality at my study site in spring is linked to recent snake emergence from hibernation, then the timing of my surveys likely favors observing arboreal behavior in cottonmouths, while the timing of Graham's (2013) surveys does not. Graham (2013) does, however, provide evidence of arboreal behavior by cottonmouths in spring. On 1 March, Graham (2013) observed a group of approximately six *A. piscivorus* in shrubs 1–1.5 m above the water near a hibernaculum. He believed the snakes had been forced into shrubs by high water. The snakes may have been exhibiting arboreal behavior similar to that I observed in southern Illinois. Regardless of the explanation for the differences in our observations, the results of my study demonstrate that arboreal behavior by cottonmouths can be frequent and is not a "myth" (Graham 2013, p. 430).

ACKNOWLEDGEMENTS

The comments of Steve Mullin, members of the Eastern Illinois University herpetology laboratory, and three anonymous reviewers improved the manuscript. I dedicate this work to Erin Palmer who contributed to the publication of this paper.

LITERATURE CITED

Adolph, S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315–327.

Allen, E.R. and D. Swindell. 1948. Cottonmouth moccasin of Florida. Herpetologica 4 (Supplement 1): 1–16.

Avery, R.A. 1982. Field studies of body temperatures and thermoregulation. pp. 93–166. In Biology of the Reptilia, Volume 12, Physiology C Physiological Ecology. Gans C. and F.H. Pough (Eds.). Academic Press, London

Beaupre, S.J. 1995. Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. Ecology 76:1655–1665.

Blem, C.R. and L.B. Blem. 1995. The eastern cottonmouth (*Agkistrodon piscivorus*) at the northern edge of its range. Journal of Herpetology 29:391–398.

Cagle, F.R. 1942. Herpetofauna of Jackson and Union counties, Illinois. American Midland Naturalist 28:164–200.

Changnon, S.A., J.R. Angel, K.E. Kunkel, and C.M.B. Lehmann. 2004. Climate Atlas of Illinois. Illinois State Water Survey, Champaign.

Crane, A.L. and B.D. Greene. 2008. The effect of reproductive condition on thermoregulation in female *Agkistrodon piscivorus* near the northwestern range limit. Herpetologica 64:156–167.

Dundee, H.A. and D.A. Rossman. 1989. The Amphibians and Reptiles of Louisiana. Louisiana State University Press, Baton Rouge.

Dunham, A.E., B.W. Grant, and K.L. Overall. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiological Zoology 62:335–355.

Ernst, C.H. and E.M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Institution, Washington, DC.

Finkler, M.S. and D.L. Claussen. 1999. Influence of temperature, body size, and inter-individual variation on forced and voluntary swimming and crawling speeds in *Nerodia sipedon* and *Regina septemvittata*. Journal of Herpetology 33:62–71.

Garman, H. 1892. A synopsis of the reptiles and amphibians of Illinois. Illinois Laboratory Natural History Bulletin 3(13):215–388.

Geiger, R. 1965. The Climate Near the Ground. Harvard University Press, Cambridge, Massachusetts.

Gibbons, W. and M. Dorcas. 2005. Snakes of the Southeast. University of Georgia Press, Athens.

Gloyd, H.K. and R. Conant. 1990. Snakes of the *Agkistrodon* complex. Society for the Study of Amphibians and Reptiles. Contributions to Herpetology 6:1–614.

Graham, S.P. 2013. How frequently do cottonmouths (*Agkistrodon piscivorus*) bask in trees? Journal of Herpetology 47:428–431.

Gregory, P.T. 1982. Reptilian hibernation. Pp. 53–154 In Biology of the Reptilia, Volume 13, Physiology D Physiological Ecology. Gans, C. and F.H. Pough (Eds.). Academic Press, London.

Gregory, P.T. 1984. Communal denning in snakes. pp. 57–75 In Vertebrate Ecology and Systematics, A Tribute to Henry S. Fitch. Seigel, R.A., L.E. Hunt, J.L. Knight, L. Malaret, and N.L. Zuschlag (Eds.). Museum of Natural History, The University of Kansas, Lawrence.

Harmeson, R.H. and V.M. Schnepper. 1965. Temperatures of surface waters in Illinois. Illinois State Water Survey Report of Investigation 49.

Hollinger, S.E. and S.A. Isard. 1994. A soil moisture climatology of Illinois. Journal of Climate 7:822–833.

Lillywhite, H.B. 2014. How Snakes Work: Structure, Function and Behavior of the World's Snakes. Oxford University Press, Oxford, United Kingdom.

Lillywhite, H.B. and R.J.R. McCleary. 2008. Trophic ecology of insular cottonmouth snakes: review and perspective. South American Journal of Herpetology 3:175-185.

MacKinnon, C.A., A. Lawson, E.D. Stevens, and R.J. Brooks. 2006. Body temperature fluctuations in free-ranging eastern fox snakes (*Elaphe gloydi*) during cold-water swimming. Canadian Journal of Zoology 84:9–19.

Nelson, K.J. and P.T. Gregory. 2000. Activity patterns of garter snakes, *Thamnophis sirtalis*, in relation to weather conditions at a fish hatchery on Vancouver Island, British Columbia. Journal of Herpetology 34:32–40.

Olsson, M., T. Madsen, and R. Shine. 1997. Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. Proceedings of the Royal Society of London 264:455–459.

Palis, J.G. 2010. A non-disruptive assessment of a southern Illinois snake den 60 years after Conway. Proceedings of the Indiana Academy of Science 119:74–79.

Peterson, C.R., A.R. Gibson, and M.E. Dorcas. 1993. Snake thermal ecology: the causes and consequences of body temperature variation. Pp. 241–314. In Snakes Ecology and Behavior. Seigel, R.A.and J.T. Collins (Eds.). McGraw-Hill, Inc., New York, New York.

Prior, K.A. and P.J. Weatherhead. 1996. Habitat features of black rat snake hibernacula in Ontario. Journal of Herpetology 30:211–218.

Roberston, I.C. and P.J. Weatherhead. 1992. The role of temperature in microhabitat selection by northern water snakes (*Nerodia sipedon*). Canadian Journal of Zoology 70:417–422.

Rossman, D.A. 1960. Herpetofaunal survey of the Pine Hills area of southern Illinois. Journal of the Florida Academy of Sciences 22:207–225.

Row, J.T. and G. Blouin-Demers. 2006. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milksnakes. Oecologia 148:1–11.

Sears, M.W. 2005. Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity. Oecologia 143:25–36.

Smith, P.W. 1961. The Amphibians and Reptiles of Illinois. Illinois Natural History Survey Bulletin, Volume 28, Article 1.

Stevenson, R.D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. American Naturalist 126:362– 386.

Stevenson, R.D., C.R. Peterson, and J.S. Tsuji. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. Physiological Zoology. 58:46–57.

Terres, J.K. 1991. The Audubon Society Encyclopedia of North American Birds. Wing Books, New York, New York.

Tiebout, H.M. and J.R. Cary.1987. Dynamic spatial ecology of the watersnake, *Nerodia sipedon*. Copeia 1987:1–18.

Weatherhead, P.J. and I.C. Robertson. 1992. Thermal constraints on swimming performance and escape response of northern water snakes (*Nerodia sipedon*). Canadian Journal of Zoology70:94–98.

Weatherhead, P.J., J.H. Sperry, G.L.F. Carfagno, and G. Blouin-Demers.2012. Latitudinal variation in thermal ecology of North American rat snakes and its implications for the effect of climate warming on snakes. Journal of Thermal Biology 37:273–281.