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USE OF SPACE BY WESTERN COTTONMOUTHS (*AGKISTRODON PISCIVORUS*) INHABITING A VARIABLE-FLOW STREAM

FRANCIS L. ROSE,* THOMAS R. SIMPSON, JAMES R. OTT, AND RICHARD W. MANNING

Department of Biology, Texas State University-San Marcos, San Marcos, TX 78666
Present address of RWM: 107 LBJ Cove, San Marcos, TX 78666
**Correspondent: fr02@txstate.edu*

ABSTRACT—In central Texas, western cottonmouths (*Agkistrodon piscivorus*) inhabit small, low-productivity limestone streams characterized by variability in seasonal flows. An 11-year study of western cottonmouths was conducted at Honey Creek, a spring-fed stream flowing 3.2 km to its confluence with the Guadalupe River, Comal County, to determine how this predator used space in this narrow, linear, and dynamic system. During 57 searches along the 1,564-m study area, 39 sexually mature, 14 subadults, and 4 juvenile snakes were marked. Rates of recapture did not differ between sexes, but females outnumbered males (2.3:1) and adults were recaptured more frequently than juveniles. Distances between captures were less than predicted if distributions were random, and distances did not vary with number of times captured or time between captures.

RESUMEN—En Texas central, la mocasín boca de algodón (*Agkistrodon piscivorus*) habita en pequeñas corrientes de baja productividad con lecho de piedra caliza caracterizadas por variabilidad en flujos estacionales. Un estudio de 11 años de la mocasín boca de algodón fue realizado en Honey Creek, una corriente, alimentada por manantiales, que fluye 3.2 km a su confluencia con el río Guadalupe, condado de Comal, para determinar cómo este depredador usó espacio en este sistema estrecho, lineal y dinámico. Durante 57 muestreos a lo largo del área de estudio de 1,564 m, 39 adultos sexualmente maduros, 14 subadultos y 4 juveniles fueron marcados. Las tasas de recaptura no variaron entre los sexos, pero hubo más hembras que machos (2.3:1) y los adultos fueron recapturados más frecuentemente que los juveniles. Las distancias entre capturas fueron menos que lo pronosticado (si las distribuciones fueran aleatorias), y las distancias no variaron con el número de capturas, ni con el tiempo entre capturas.

Although movement patterns of snakes have been studied extensively (Macartney et al., 1988), Diffendorfer et al. (2005) stated that we are still in the formative stages of understanding spatial patterns of snakes. Willson et al. (2006) analyzed post-drought patterns of movement in several semi-aquatic snakes, including the eastern cottonmouth in a wetland in South Carolina, and Glaudas et al. (2007) evaluated migrational patterns of cottonmouths in the same wetlands. Both studies confirmed extensive movements of eastern cottonmouths associated with droughts in a wetland.

Western cottonmouths, *Agkistrodon piscivorus*, are pit vipers that inhabit a wide variety of habitats (Gloyd and Conant, 1990; Werler and Dixon, 2000). The species is ubiquitous in the eastern one-half of Texas and occurs from coastal marshes to inland streams (Werler and Dixon, 2000). Little is known about the ecology, demography, or population biology of this subspecies in central Texas, where it may be in small shallow streams (Ramsey, 1948; Hicks, 1995). Some of these streams form a narrow inhabitable corridor that is surrounded by more xeric environments that lack life-sustaining resources for semi-aquatic snakes. Extreme variation in seasonal flows, characteristic of small streams in central Texas, suggests that individuals inhabiting these systems may be subject to rapid turnover and redistribution (Rose et al., 2010). Because western cottonmouths inhabit such a variety of habitats, and are much more terrestrial than generally believed, they may be significant predators of fish, amphibians, mammals, birds, and other reptiles (Savitzky, 1992). It is, thus, important to understand how these snakes use space over time because many habitats that they occupy, notably those characterized by pulsing environments, e.g., streams, rivers, and ephemeral ponds, are influenced by humans. In addition, understanding patterns in use of space over multiple years enhances our understanding of spacial needs and increases our ability to effectively manage populations. Management practices based on short-term studies of iteroparous organisms might lack sufficient and critical information to accurately assess environmental needs.

We present results of an 11-year, mark-recapture study focusing on use of space by western cottonmouths inhabiting a linear system composed of a small, highly variable, and low-productivity stream in central Texas. We predicted that the position of an individual western cottonmouth would be random over time in the system because of displacement by extreme environmental perturbations that included high-amplitude pulses of flood and droughts. We further predicted that there would be a net movement of snakes downstream because of flood pulses and that presence of a snake in the system would be short-lived.

Materials and Methods—Honey Creek emanates from Honey Creek Cave (UTM Zone 14 coordinates 549681 Easting and 3303260 Northing) in Comal County, Texas, and is contained within the Honey Creek State Natural Area (Rose et al., 2010). Secondary springs increase flow along its 3.2-km course to the Guadalupe River. The limestone, spring-fed stream runs in a rocky bed (typically 3–5 m wide) that alternates between three deep pools and shallow riffles meandering among roots of bald cypresses (*Taxodium distichum*). Along parts of the stream, steep rock walls ≤17 m high occur within meters of the stream, while at other points the stream broadens and banks slope upward at 15–25° to arid uplands of rocky soils with oak (*Quercus fusiformis*, *Q. buckleyi*)-juniper (*Juniperus ashei*) woodlands and an understory of Texas persimmon (*Diospyros texana*). A dense overstory limits penetration of sunlight along the stream. During times of flow in spring, temperature of water was 20–23°C.

Rain events in the Honey Creek watershed generate large-amplitude variation in hydrologic conditions. On nine occasions during our study, flows at the Guadalupe River Spring Branch Gauging Station were >3,080 cubic m/s (United States Geological Survey 08,167,500; Water Resources Data-Texas for water years 1992–2003). The gauging station is 6.5 km from the study site and each event was associated with flooding at Honey Creek, increasing depth of water to 5.2 m. There was a period of no flow in 1999, but the most-severe drought occurred in 2000 when flow from the cave ceased, and all but the three pools were dry for most of May–September. Substantial flow returned in early May 2001.

We selected a 684-m segment of stream (Area 1) beginning at the opening of Honey Creek Cave to survey snakes in 1992. This headwater section of the stream represented 21% of its 3.2-km length measured from origin to confluence with the Guadalupe River. The search area was extended 880 m downstream (Area 2) in 1995 to ascertain whether marked snakes that were not recaptured had established activity areas beyond the initial study site. We surveyed for snakes on average 4.4 times (range, 2–8) during May–September each year in 1992–2003. For each survey, two to five individuals (mean = 3.2) searched the full length of the study area up to the shear vertical cliffs. Surveys were conducted during 1100–1500 h (51 times) or 2000–0200 h (6 times). A total of 57 surveys was conducted with an average of 2.3 h expended/survey for a total effort of 418.3 h.

Snakes were captured with tongs and their snout–vent length and mass were recorded. Sex was determined by probing the vent. A snout–vent length ≥50 cm indicated sexual maturity (Burkett, 1966; Ford, 2002; Hampton and Ford, 2005). Snakes <50 cm in snout–vent length were considered to be subadults. Juveniles were defined as subadults of smaller size with a distinctive color and body pattern (Gloyd and Conant, 1990), including presence of a conspicuous yellow-tipped tail (Neill, 1960). Each snake was injected with a PIT-tag, scale-clipped in case of failure of the PIT-tag, and released at site of capture. Position of capture was the number of meters downstream from the opening of the cave as measured from structures in the landscape that were of known distance using a tape measure. Data are presented as mean ± *SD* and range (in parentheses).

Linear-spatial data for recaptures were evaluated in two primary ways to pattern the positions of marked snakes within the system: distance between successive captures and distance of each site of capture from the mean site of capture for each snake. Snakes that were caught only twice in one season were eliminated from analyses. This provided a dataset of 9 males and 20 females with multiple captures within years, among years, or both.

We generated a distribution of distances between sites of recapture under a simulated model to determine whether distances between captures were less between successive recaptures than expected based on a stochastic model of random movement with limited sampling. We partitioned the stream into 1-m increments for the 1,564-m length of the study area. We then randomly generated numbers from a uniform distribution (random.org/nform.html) to simulate possible sites of capture, with a minimum value of 0 m and a maximum value of 1,564 m for each of 10 hypothetical snakes (i.e., replicates), each captured 2–11 times, sampling with replacement. We calculated mean number of meters between sites of recapture for each number of recaptures, ran the test 20 times, and averaged the estimates. We used a one-tailed *t*-test to test for differences in distances between captures of snakes and estimated distances generated through the stochastic model.

Distances moved between captures do not elucidate direction of movement or the physical position of snakes in the stream. To evaluate use of space by each snake, recaptures for each snake were plotted on a map of the stream. Mean distance of capture for each snake was calculated from the origin of the stream at the opening of Honey Creek Cave. Distances for each capture from the mean were calculated and the mean of those distances were determined for each snake.

RESULTS—Of all western cottonmouths observed during 57 surveys, 94% (166 of 177) were captured, but only 2.7 ± 2.2 (0–11) snakes were captured/survey. This translated into a rate of 1 snake/246 m of stream searched during 1992–1995, and 1 snake/564 m of stream searched during 1995–2003. Snakes were captured at the rate of 1/2.5 h of effort. Western cottonmouths at Honey Creek, thus, were encountered infrequently.

Recaptures—We captured 57 snakes 130 times, 21 (37%) snakes were not recaptured, 25% were captured ≥4 times, and 1 was captured 11 times. There was no difference in rates of recapture for adult males (75%) and females (77%). Subadults, however, were less likely than adults to be recaptured with only 28% being recaptured ($\chi^2 = 9.79$, $df = 1$, $P = 0.001$). Only one juvenile was captured twice and it was not observed as an adult. The greatest number of intervening years between captures was 9 (one individual); there was 291 h of searching between when this animal was captured and its first recapture. For number of years between captures, 10 individuals had 1 year, 6 had 2 years, 5 had 3 years, and 1 had 4 years.

Structure of Population—Of the 57 marked snakes, 39 (68%) were sexually mature (≥50 cm snout–vent length), 14 (25%) were subadults, and only 4 (7%) were juveniles. Sex ratio of mature animals was 2.3 females:1 male. Based on data obtained at first capture for sexually mature individuals, males ($n = 13$) had a mean snout–vent length of 63.4 ± 69.6 cm (range, 53.5–73.0) and a mean mass of 277 ± 78.7 g (range, 165–415). Females ($n = 26$) had a mean snout–vent length of 59.9 ± 43.6 cm (range, 515–660) and a mean mass of 258 ± 60.7 g (range, 155–370). Although 33% of males exceeded the greatest snout–vent length of females, the difference was not significant ($t = -1.920$, $df = 37$, $P = 0.063$), and mass did not differ between sexes ($t = -0.839$, $df = 37$, $P = 0.407$).

Fidelity to Site—The mean distance (m) between captures inclusive of recaptures within and among years of males was greater than that of females: males = 316 ± 236 (range, 62–684); females = 157 ± 120 (range, 8–436; $t = -2.420$, $df = 27$, $P = 0.020$). Because the number of males was low (nine) and, as presented later, there was no difference between sexes when mean distance from the mean site of capture was evaluated, and because combining data did not affect outcome of any parameter we investigated, we pooled data for males and females for further analyses. Distance between captures did not vary with number of times recaptured (Fig. 1) or with number of years between captures (Fig. 2). Mean distance between captures of individual snakes was 160 m; whereas the mean of the estimated distances based on the simulated model was 527 m (Fig. 1). The difference was significant ($t = -9.010$, $df = 15$, $P < 0.001$). The longest mean distance between captures was 276 m.

Average distance from mean site of capture for males ($n = 9$) was 119 m and for females ($n = 20$) it was 125 m. Means did not differ from unity ($t = 0.140$, $df = 27$, $P = 0.880$). Mean distance between captures for all snakes was 121 ± 92 m (range, 0–315). Only one of the nine mean values calculated for males exceeded the mean plus one standard deviation for the sample of females. Figure 3 depicts mean distances from the mean site of capture plotted against number of times captured, indicating that area of use by individual snakes did not increase with number of times captured. The lack of significant positive relationships between distance moved and times captured and years between captures suggests that some snakes in this system exhibit limited movements within seasons and do not appear to shift their activity ranges annually.

Spacial Pattern—Regarding pattern in use of space, western cottonmouths were aggregated. Snakes were observed most frequently in brush piles over running water (49%) during day, while at night they frequently were coiled or active at the edge of water between pools. They frequently were captured at the downstream end of deep pools where debris (basking sites) accumulated after floods. Occurrence was lowest on edges of pools and highest occurrence was at Bell Springs, where two springs converged. Only one snake was captured well away (25 m) from water among boulders. More snakes (19%) were captured at night (10% of visits) per unit effort.

Polarity of Movements—In Study Area 1, 40 snakes were captured initially; 6 (15%) were recaptured in Study Area 2. In Study Area 2, 17

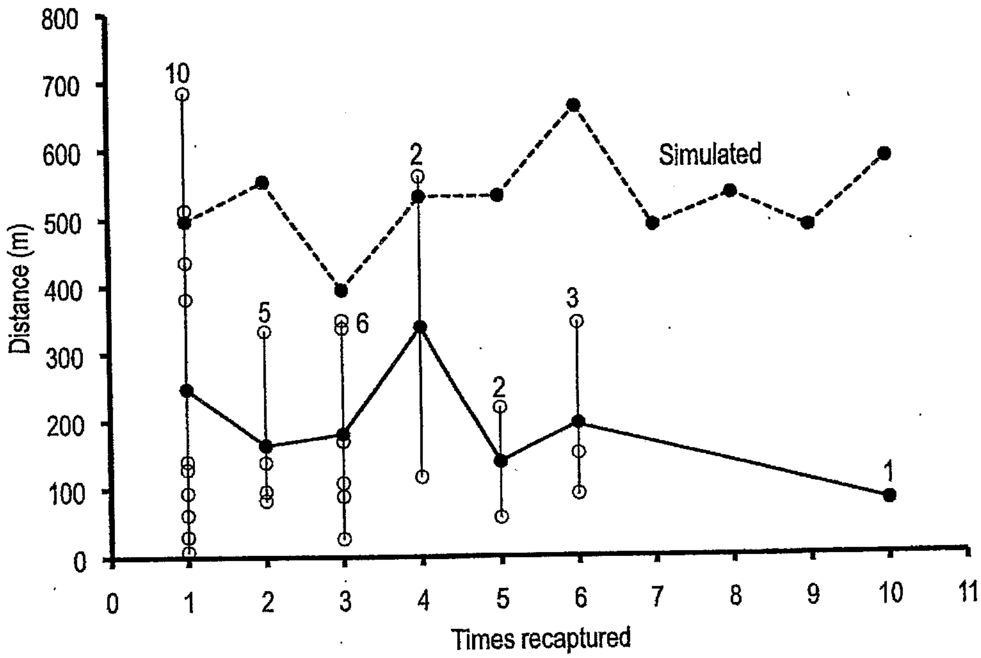

FIG. 1—Distance between captures of western cottonmouths (*Agkistrodon piscivorus*) recaptured 1–10 times at Honey Creek, Comal County, Texas. Open circles represent mean distance for each snake, solid circles represent the mean for each set of snakes, and solid circles along the dashed line represent means of 20 simulated distances between captures of snakes that were recaptured 1–10 times. Size of samples are at the top of each plot.

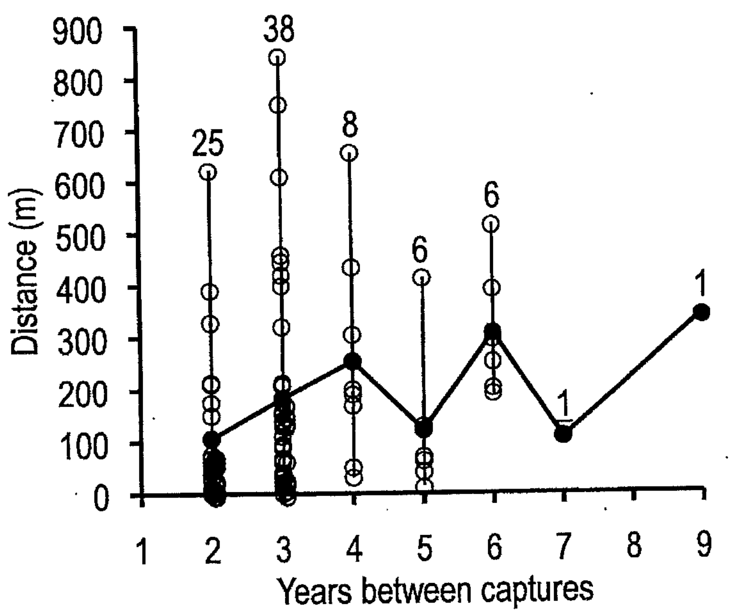

FIG. 2—Mean distances between captures of western cottonmouths (*Agkistrodon piscivorus*) at Honey Creek, Comal County, Texas, plotted against number of years between captures. Each open circle represents the mean for each snake and solid circles represent the mean for each set. Size of samples are at the top of each plot.

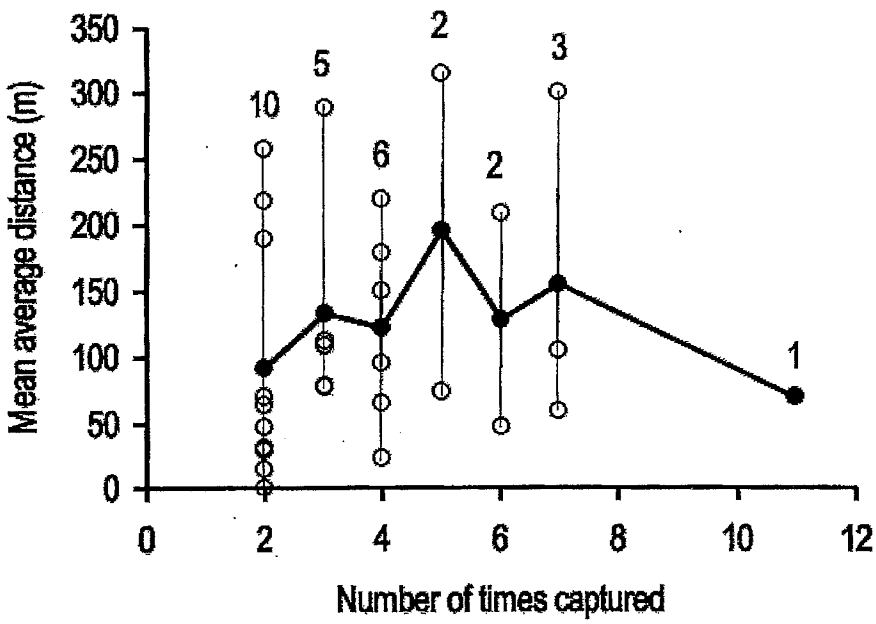

FIG. 3—Mean distance from the mean for western cottonmouths (*Agkistrodon piscivorus*) captured two or more times at Honey Creek, Comal County, Texas. Open circles represent mean distance from the mean for each snake and solid circles represent the mean for each set. Size of samples are at the top of each plot.

snakes were captured initially: 4 (23%) were recaptured at least once in Study Area 1. Three of these were captured initially at or near the junction of the two study sites and were caught subsequently in both areas. Eight snakes captured ≥2 times moved only downstream of the initial site of capture, five moved only upstream, and six moved in both directions.

DISCUSSION—There are three primary patterns of how organisms associate in space: random, aggregated, and overdispersed (reviewed by Gregory et al., 1987). Western cottonmouths at Honey Creek were aggregated, presumably because basking sites and direct solar radiation were limited. Basking sites, as a resource, probably account for the limited use of space by individual snakes in this system.

Tinkle (1979) outlined the value of long-term studies of populations and of the factors limiting their investigation, and Macartney et al. (1988) noted that patterns in use of space by snakes might be evident if studies were done over longer periods. Time constraints and effort are weighed against statistically significant returns. There is, thus, a tendency to study populations at relatively high densities, preferably with high rates of turnover, because they provide readily available information; yet, many populations are not dense, and densities vary throughout the geographic range of a species. Radiotelemetry provides an avenue to assess short-term and long-term patterns of movement (Diffendorfer et al., 2005), but constraints of cost and time might limit samples to small subsets of populations. Diffendorfer et al. (2005) cautioned against using means to describe data on movement because they obscure relationships and impacts of some snakes that make extreme movements. We agree with this cautionary statement, but we were not interested in comparative movements of individuals, and we used distance to delineate position along the stream. A few snakes at Honey Creek made extensive movements and established new areas of activity, but most that remained in the system did so in a limited area, some over long periods, while being subjected to extreme environmental fluctuations in hydrologic conditions. Limited movements of snakes out of each study area, upstream or downstream, further support the finding that many recaptured western cottonmouths used space at

Honey Creek at a level below what was expected if locations of captures were random, or if there were extensive redistributions following floods or droughts.

Sex ratios of adult western cottonmouths at Honey Creek deviated from 1:1, favoring females. Ford (2002) noted that the sex ratio in his population did not vary from equity. Although Roth (2005*a*) did not report sex ratios, he noted that five adult male cottonmouths that he telemetered had larger home ranges than did five gravid and five non-gravid females. He concluded that after controlling for body size, this difference remained. Hill and Beaupre (2008) reported a 1:1 sex ratio for western cottonmouths inhabiting a riffle-pool creek system in northern Arkansas. They noted that mean size of members of this population was the smallest recorded. The population of snakes at Honey Creek is comparable in size, except the mass of females at Honey Creek is 15% greater than females in the population studied in Arkansas. Given that reproductive schemes of females in both populations might be different, which might affect weights, we posit that members of the two populations do not differ significantly in size.

We noted no substantial difference between sexes in distances between captures at Honey Creek. This may be, as Roth (2005*b*) pointed out, that in linear systems resources are less scattered in space, and time spent and distance traveled for those resources might be less. Females are resources for males and males might travel considerable distances in search of that resource. In populations where adult females significantly outnumber males, such as at Honey Creek, intersexual differences in spatial patterns might be muted.

Several authors commented on terrestrial activity of cottonmouths (Allen and Swindell, 1948; Dundee and Burger, 1948; Hamilton and Pollack, 1955). Eastern cottonmouths on Sea Horse Key (Wharton, 1969; Lillywhite et al., 2008) rarely have access to fresh water. Long-term associations with droughts and migrations to avoid their effects have equipped cottonmouths with physiological tolerances that allow them to exploit terrestrial environments and to capitalize on a variety of prey, living and scavenged (Wharton, 1969). We emphasize that habitat away from and above Honey Creek can be extremely dry and the three pools maintained water throughout our study, eliminating the need for cottonmouths to migrate away from the streambed, even during droughts. Unmarked snakes were captured throughout the study, implying that the population was not static; yet, some snakes were long-term residents as they were captured over several years.

Pattishall and Cundall (2008) reported on 50 telemetered northern watersnakes, *Nerodia sipedon*, inhabiting an urban stream in Pennsylvania. The snakes exhibited high fidelity to sites, with 82% of relocations being within a 1-m radius of the previous locality. Further, when snakes moved to other sites, 56% returned to previously occupied sites. Similar to western cottonmouths at Honey Creek, some of the northern watersnakes returned to previous areas of activity after being displaced by a flood.

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