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Cover Photograph: Peeking out is "Hooty", a copperhead that remained in a root hole in a manicured section of Overton Park, Memphis, Tennessee, for the month of July 2015. The hole afforded Hooty the opportunity to watch cyclists, runners, and walkers on the nearby pedestrian road and a peek of the children's playground. Hooty's transmitter stopped sending signals the following spring, but he was once again spotted in the same hole the following July. Park users seemed oblivious to his presence. Photograph © Melissa McMasters.

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Cozy in the City: The Morphology and Spatial Ecology of Copperheads in an Urban Forest

Malle F. Carrasco-Harris[1*], Judith A. Cole[1], and Steve Reichling[2]

Abstract - Anthropogenic environments alter behaviors in a wide variety of taxa. We examined the morphology and spatial ecology of *Agkistrodon contortrix* Linnaeus (Eastern Copperhead) within an urban forest and a rural forest in Tennessee. We captured snakes for morphological data and radio tracked 36 urban and 8 rural subjects to collect spatial data. We estimated home range size, core area, and movement parameters (total distance moved; daily, sampling, and monthly movement) using relocation data. Copperheads in the urban forest were smaller but did not differ in body condition compared to rural conspecifics. We found urban Copperheads had reduced home ranges, core areas, and movement parameters compared to rural subjects. Our study suggests urban snakes alter spatial behavior by decreasing overall movement.

Introduction

Urban and suburban areas are growing, leading to increasingly isolated and fragmented natural habitats surrounded by varying degrees of disturbance (Fischer and Lindenmayer 2007, United Nations 2018). Natural areas allocated for human recreation within urban settings can function as refuges for a variety of species (Dickman 1987, Harden et al. 2009, Mahan and O'Connell 2005). These habitats differ from continuous areas, as they experience the consequences of surrounding anthropogenic disturbances, including impervious land cover, exotic species introduction, wildlife subsidization, disease transfer, and human persecution (Bar-Massada et al. 2014, Fischer et al. 2012, Mitchell and Jung Brown 2008). As urban sprawl and human population density increase, native species richness and biodiversity decrease (Haddad et al. 2015, McKinney 2008). Animals persisting in these environments often have a degree of behavioral plasticity or traits that allow them to tolerate the disturbances in urban environments, such as modifying spatial, breeding, or activity behavior (French et al. 2018, Lowry et al. 2013). For example, research indicates mammals and birds decrease home range size and occur at higher population densities in urban settings because of factors such as resource availability, changes in competition, and habitat structure (Mannan and Boal 2000, Marks and Bloomfield 2006, Rutz 2006, Šálek et al. 2015, White et al. 2006).

Although mammals and birds are well-studied, less work has focused on snake behavior and spatial ecology in urban environments, despite their sensitivity to habitat modification (Burger et al. 2012), population decline (Reading et al. 2010), and human persecution (Mitchell and Jung Brown 2008). Reptile species persist in urban areas if there are favorable habitat conditions, such as connectivity between fragments, prey populations, appropriate basking and shelter locations, and structures for hibernation (Ackley and Meylan 2010, Bonnet et al. 2016, Zappalorti and Mitchell 2008). However, anthropogenic disturbances, such as roads and railways, have effects on reptile movement and survival and limit dispersal (Andrews et al. 2008, Rautsaw et al. 2018). Snakes and other reptiles in fragmented and disturbed areas tend to have smaller home ranges (Breininger et al. 2011, Lomas et al. 2019),

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alter concealment and movement patterns (Beale et al. 2016, Ferronato et al. 2015, Martin et al. 2017), and may exhibit lower body conditions (Lomas et al. 2015) compared to snakes in undisturbed areas. Taken together, these consequences may come at a cost to growth, survivability, and prey acquisition in reptiles persisting in human-disturbed environments.

Agkistrodon contortrix (Linnaeus) (Eastern Copperhead) are widespread across the eastern United States (Ernst 1992), and their distribution overlaps with a variety of other snake species that may be of greater conservation interest (Ernst and Ernst 2011). Copperheads are relatively long-lived and exhibit fidelity to seasonal sites, which makes them particularly susceptible to habitat modification (Burger et al. 2012, Fitch 1960). Hence, this species could serve as a management indicator of environments suitable for snakes and ecologically similar species (Caro and O'Doherty 1999, Levine 2013). To study the consequences of urbanization on snake spatial ecology, we conducted a longitudinal radio telemetry study on Copperheads within an urban forest. Copperhead home range and movement patterns have been characterized by radio telemetry in less disturbed settings (Rodriguez 2010, Smith et al. 2009, Sutton et al. 2017), but their spatial ecology in urban fragments has not been addressed. Understanding this common species will allow for better management of this and related species in urban natural areas, and help elucidate the effects of urbanization on herpetofauna. Our main objectives were to determine if there were differences in the morphology and spatial ecology of Copperheads within an isolated urban natural fragment and a rural forest. We expected subjects within the urban fragment would be smaller and in poorer body condition, have reduced home range size, and move less than conspecifics living in the rural forest. We also expected urban home range sizes to be smaller than previously reported for this species.

Materials and Methods

Study Sites

We studied Copperheads in Overton Park (Overton; urban forest), Memphis, TN, and Edward J. Meeman Biological Station (Meeman; rural forest), Shelby County, TN. Overton (138 hectares [ha]) is a popular recreational area at the core of the community. Within the park is a 57 ha old-growth mixed forest containing paved and unpaved trails, a golf course and clubhouse, zoo, playgrounds, dog park, art gallery, and art school. The park has been bordered by roads and residential and commercial areas for over a century (Bearden 2004). The park and forest within it support a subset of native herpetofauna, including Copperheads (Davis et al. 2012). Meeman (252 ha) is a University of Memphis property dedicated to scientific study located 24 km north of Overton and composed of deciduous, evergreen, and mixed forest, as well as some pastures. It is bordered by private and public forest and woody wetlands. There are a few small buildings, and a low-traffic road bisects the property; a state park and private land border the area. Meeman is not open to the public and does not have an extensive trail network, making it relatively less disturbed than Overton.

Capture and Surgery

We captured 243 Copperheads (Table 1) by hand during visual searches, or when found with focal subjects (tracked animals) and by using drift fences with funnel box traps. We transported animals in a secured container to the Memphis Zoo veterinary hospital for morphological data collection and surgical implantation of radio transmitters. All subjects were included in the basic data collection, and a subset was included in radio telemetry research. We safely restrained animals in an acrylic tube and injected a passive-integrated transponder

(PIT) tag (134.2 kHz 8.4 mm Biomark, Boise, ID) ~10 cm anterior to the cloaca for individual identification. We used the last 4 characters of the PIT tag identification number for all records associated with a subject and noted recaptures when a previously caught individual was identified. We photographed subjects with a standard for digital measurement of snout-vent length (SVL; ± 0.01 cm) using ImageJ (National Institutes of Health, Bethesda, MD) and recorded mass on a digital scale (± 0.01 g; HX-502 American Weigh Scales, Norcross, GA). We determined sex by probing for the presence of hemipenes in males, and we palpated adult females to detect ova.

We estimated body condition, an indicator of health, by calculating the scaled mass index (SMI) for each animal following the methods of Peig and Green (2009, 2010). This index incorporates allometric changes in scaling observed in many species and outperforms other methods of determining body condition (Peig and Green 2010). Briefly, we used standardized major axis (SMA) regression (Warton et al. 2012) to create a line of best fit for the natural log-transformed mass and SVL of males and non-gravid females. The SMA regression accounts for error in both variables (mass and length). We used the slope of the SMA regression, mass, length, and mean population length to calculate the SMI for each individual. Individual SMI can be compared between groups or to the population average. We excluded gravid females from morphological analyses because they are expected to be heavier for their length than predicted.

The senior zoo veterinarian and staff surgically implanted radio transmitters (R1680 3.6 g, Advanced Telemetry Systems, Isanti, MN) into selected adult subjects following methods adapted from Reinert and Cundall (1982). Transmitters weighed less than 5% of body mass. We monitored subjects at the hospital for 24 h post-implantation and assessed behavior and the surgical site incision before release at their capture location. We surgically removed transmitters from all animals that could be located after 1 year and returned the snakes to their final relocation site.

Radio Telemetry and Spatial Analyses

From June 2015 to July 2018, we radio-tracked 44 subjects (25 males, 19 females) twice per week during the active season (15 March–15 November). After implantation and release, the snakes were located by using a hand-held 2-element RA-23K VHF antenna (Telonics, Mesa, AZ) or 3-element folding Yagi antenna (Advanced Telemetry Systems, Isanti, MN) with an R-1000 telemetry receiver (Communications Specialists, Orange, CA),

Table 1. Copperhead snakes captured at urban Overton Park and rural Meeman Biological Station. Trap implies animal found in funnel trap array. Opportunistic animals were captured outside of traps by researcher.

		Capture		
Location	Sex	Trap	Opportunistic	Total
Meeman	M	11	5	16
	F	1	8	9
Overton	M	44	65	109
	F	30	78	108
	NA*	1	0	1
		87	156	243

*Unable to sex small animal.

and their positions were identified (i.e., relocated). We separated consecutive relocations by 3–4 days to reduce spatial autocorrelation (White and Garrott 1990) since snakes use localized areas for extended periods of time (Row and Blouin-Demers 2006). The median number of active season relocations was 51 (range 11–64). We obtained geographic coordinates of the animal location using a hand-held global positioning system (±5 m; GPSmap 76Cx, Garmin, Olathe, KS) or triangulated the location if the animal could not be seen because of dense vegetation. We recorded temperature and humidity at each relocation using a psychrometer (Temperature Pen 800012, Sper Scientific, Scottsdale, AZ).

We estimated home range sizes using minimum convex polygons (MCP), kernel density estimators (KDE), and local convex hull methods (LoCoH). We calculated home range sizes using MCP (Fig. 1) with the R package adehabitatHR (Calenge 2006, Mohr 1947). We calculated 100% and 95% MCPs to account for possible overestimation due to outliers (White and Garrott 1990). We estimated utilization distributions using fixed kernel density estimators (KDE; Fig. 1A) with the R package rhr (Signer and Balkenhol 2015, Worton 1989). Kernel utilization distributions model spatial use as a probability density function. We estimated the KDE smoothing parameter using the bivariate plug-in method, as it is robust at decreasing absolute error and is a preferable choice for studies with small-bodied taxa, such as snakes (Bauder et al. 2015). We also calculated utilization distributions using adaptive LoCoH (Fig. 1B) with the R package rhr (Getz et al. 2007, Getz and Wilmers 2004, Signer and Balkenhol 2015). The LoCoH method is advantageous because of increasing accuracy with sample size and better recognition of boundaries that are inaccessible, limiting home range estimates accordingly. For both utilization distribution methods, we bounded home ranges and core areas at 95% and 50% top use areas, respectively.

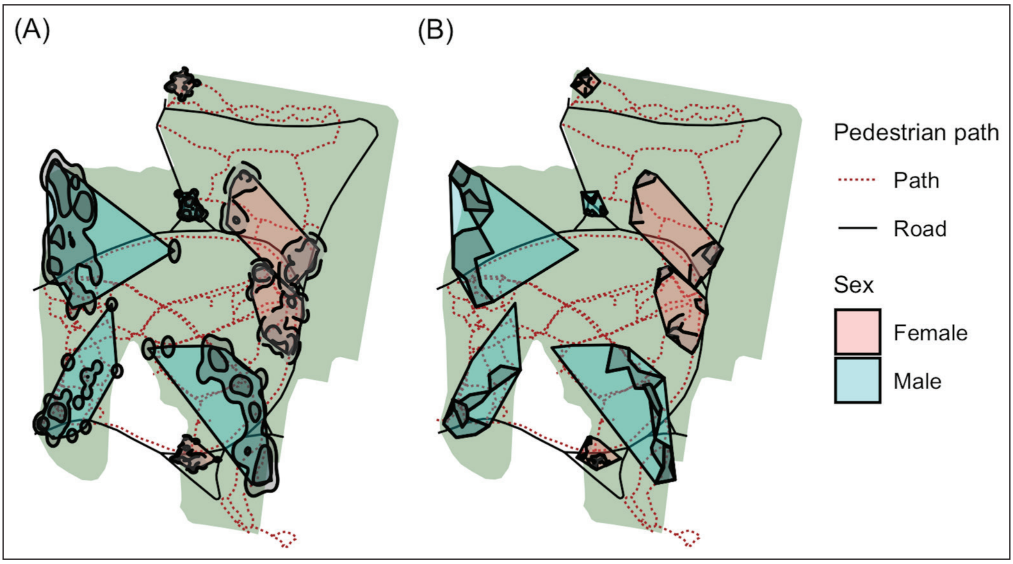

Figure 1. Home range model examples for a selection of 8 Copperhead snakes in the urban forest Overton Park. Polygons represent active season minimum convex polygon (MCP) home ranges for males and females. (A) Kernel density estimator home ranges and core areas shown within MCPs in gray. (B) Local convex hull home ranges shown within MCPs in gray. Not all individuals in the study are shown in the figure. Those displayed show a range of MCPs including the smallest and largest home ranges for both sexes as well as intermediate individuals with minimal overlapping.

We calculated movement metrics, including total distance, mean daily movement, mean movement between sampling relocations, and mean monthly movement for each snake, with the R package adehabitatLT (Calenge 2006). Total distance is the summation of the Euclidian distance between relocations. Mean daily movement is the summation of the distance between relocations divided by the number of days the animal was observed. Mean movement between sampling relocations is the summation of the distance between relocations divided by the number of observations. Mean monthly movement is the summation of distance between relocations divided by the number of observations in a month.

Statistical Analyses

Prior to statistical analyses, we followed the data exploration protocol described in Zuur et al. (2010). We assessed whether urban and rural Copperheads differed morphologically, specifically by mass, length, and scaled mass index (SMI). We used linear models (ANOVA) to determine if there were differences by location and included sex as a covariate to control for size differences between males and females (Smith et al. 2009). We compared models with and without interactions using the corrected Akaike information criterion (AICc) to select the most parsimonious model given the data (Burnham and Anderson 2002). We normalized morphological data by using the square root of mass and the natural logarithm (ln) of SMI for the analyses. Common transformations did not enhance normality for SVL; therefore, we used the raw data for analysis and verified model assumptions using residuals.

We found 100% and 95% MCP areas were highly correlated ($r = 0.95$, $P < 0.001$), and we, therefore, conducted all analyses with 100% MCP for comparability between studies. We estimated home range using 100% MCP and 95% KDE and LoCoH, and we estimated core areas using 50% KDE and LoCoH. We used linear models to determine differences in home range and core area by location and included year and sex as covariates to control for period in study and home range differences between males and females, respectively (Smith et al. 2009). We ln-transformed all home range and core area response variables in our analyses.

Further, we compared our home range estimates to other rural Copperhead populations using individual MCP home range estimates from Alabama (Sutton et al. 2017), Connecticut (Smith et al. 2009), and Nebraska (Rodriguez 2010), using a linear model with sex, location, and their interaction. We made pairwise comparisons between locations by sex and corrected significance estimates using Holm-Bonferroni multiple comparison adjustments to reduce type I error (Holm 1979). Although 2 of the studies were manipulative, they did not find significant differences between control and treatment groups for home range size (Rodriguez 2010, Sutton et al. 2017) and were, therefore, included for broader comparison purposes.

We used linear models to assess total distance moved, mean daily movement, and mean movement per sample by location and included year and sex as covariates to control for period in study and movement differences between males and females. We included the number of relocations for each individual in the analysis of total distance moved since it would be positively related to how long the subject was tracked. To determine differences in monthly movement, we used linear mixed models from the lmerTest package in R (Kuznetsova et al. 2017) and included sex, location, month, and year as fixed effects and individual as a random effect. We selected the most informative and parsimonious nested model using AIC. We conducted pairwise comparisons by consecutive months to determine if Copperhead movement differed throughout the active season using Holm-Bonferroni multiple comparison adjustments (Holm 1979). Further, we conducted pairwise comparisons of the sexes by month to determine if females and males differed in monthly movement. All movement metrics were ln-transformed to meet assumptions of normality.

We verified linear model assumptions by plotting residuals versus fitted values and each covariate in the model. If appropriate, we assessed residuals for temporal dependency (Zuur and Ieno 2016). All statistical tests were 2-tailed and accepted as significant at $P \leq 0.05$. Statistical analyses were conducted using the R programming environment v. 3.3.3 (R Core Team 2017).

Results

Capture and Morphology

We captured snakes from May 2015–August 2018, totaling 217 unique individuals out of 243 captures across both sites (Table 1). Opportunistic captures occurred at an average temperature of 26.5 ± 0.3 ˚C and humidity of 62.5 ± 1.3%. One individual at the rural forest and 25 at the urban forest were recaptured (captured and subsequently identified using their PIT tags). Nearby conspecifics were most frequently found during the breeding seasons, in particular April and July through October, but it was not uncommon to find conspecifics of the same sex within the same area in the urban forest. Of the instances where we found an urban focal (subject) female with another snake, 27 were with males, 8 were with other females, and 1 was undetermined. For focal males, 14 instances were with females, 14 with other males, and 3 were undetermined. In five instances, 2 additional conspecifics were found with a focal snake (for a total of 3 seen Copperheads). We did not find rural Copperheads with conspecifics frequently, because there were fewer focal animals, and males spent a majority of the non-breeding active season in dense vegetation. We observed focal females with a male conspecific 3 times and never with other females. We found focal males with a female 4 times and another male 1 time. In all instances, only 1 other conspecific was present.

Male snakes generally weighed more than non-gravid female snakes (Fig. 2A; Table 2), and urban snakes weighed less than rural snakes. Similarly, male snakes were longer than female snakes (Fig. 2B), and urban snakes were shorter than rural snakes. Males had lower SMI than females (Fig. 2C), but there were no differences by location. Home range size (MCP) was not related to body condition ($F_{1,32} = 0.06$, $P = 0.81$), mass ($F_{1,38} = 0.93$, $P = 0.34$), or length ($F_{1,38} = 2.0$, $P = 0.17$) when modeled with sex, location, and year. To maintain parsimonious models, these morphological indices were not included in further analyses. Morphology metrics are summarized in Supplemental Table 1 (in Supplemental File 1, available online at: https://eaglehill.us/URNAonline2/suppl-files/urna-175-Carrasco-Harris-s1.pdf).

Home Range

We tracked 19 males and 17 females ($n = 36$) at the urban forest and 6 males and 2 females ($n = 8$) at the rural forest. Summary and spatial data for individuals tracked from 2015–2018 are provided in Supplemental Tables 2 and 3 (in Supplemental File 1). We did not find differences in home range size (MCP) between non-gravid ($n = 13$) and gravid ($n = 6$) females ($F_{1,17} = 1.26$, $P = 0.28$), and we conducted all statistical analyses with females pooled to improve balance. We found males had larger home range sizes using the 95% LoCoH method, but not by the MCP or 95% KDE methods, and larger core areas by 50% KDE and LoCoH methods (Fig. 3; Table 3; Supplemental Table 4, in Supplemental File 1). Urban animals had significantly smaller home ranges and core areas than rural animals, and estimates did not differ by year (Table 3).

We compared home ranges (MCP) by sex and location with other rural Copperhead population spatial ecology studies (Table 4). We found a significant difference between home ranges by location ($F_{4,\,85} = 30.8$, $P < 0.001$), sex ($F_{1,\,85} = 23.7$, $P < 0.001$), and their interaction ($F_{4,\,85} = 2.87$, $P < 0.05$; Fig. 4). Pairwise comparisons between locations by sex revealed urban Overton females had significantly smaller home ranges than rural female snakes from Alabama, Connecticut, and Meeman (all pairwise comparisons $P < 0.05$) but not Nebraska ($P = 0.29$). Urban Overton male snakes had significantly smaller home ranges than rural males from Alabama, Connecticut, Meeman, and Nebraska (all pairwise comparisons less than $P < 0.001$).

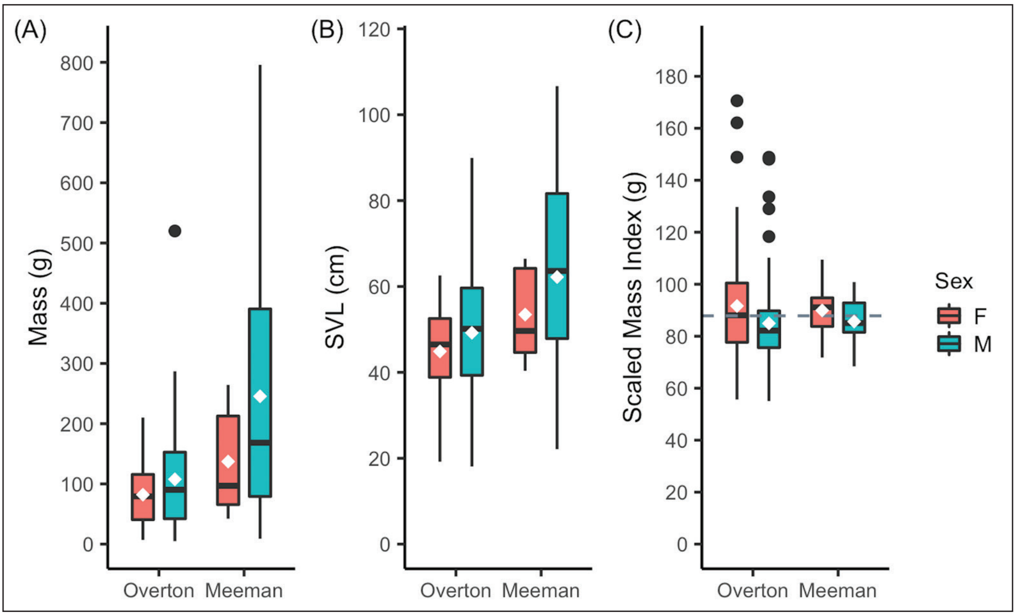

Figure 2. Morphology metrics of Copperhead snakes at urban Overton Park and rural Meeman Biological Station by location and sex. White diamonds denote means. (A) Mass in grams. (B) Snout-vent length in centimeters. (C) Scaled mass index (SMI) in grams. Dashed line represents mean SMI (87.8 g).

Table 2. Results of linear models of morphological metrics for Copperhead snakes at urban Overton Park and rural Meeman Biological Station: mass, snout-vent length (SVL), and scaled mass index (SMI).

Effect	*F*	df	*P*
Mass			
Sex	4.23	1, 198	**<0.05**
Location	16.5	1, 198	**<0.001**
SVL			
Sex	5.39	1, 197	**<0.05**
Location	12.6	1, 197	**<0.001**
SMI			
Sex	5.48	1, 197	**<0.05**
Location	0.07	1, 197	0.78

Statistically significant values are indicated in bold.

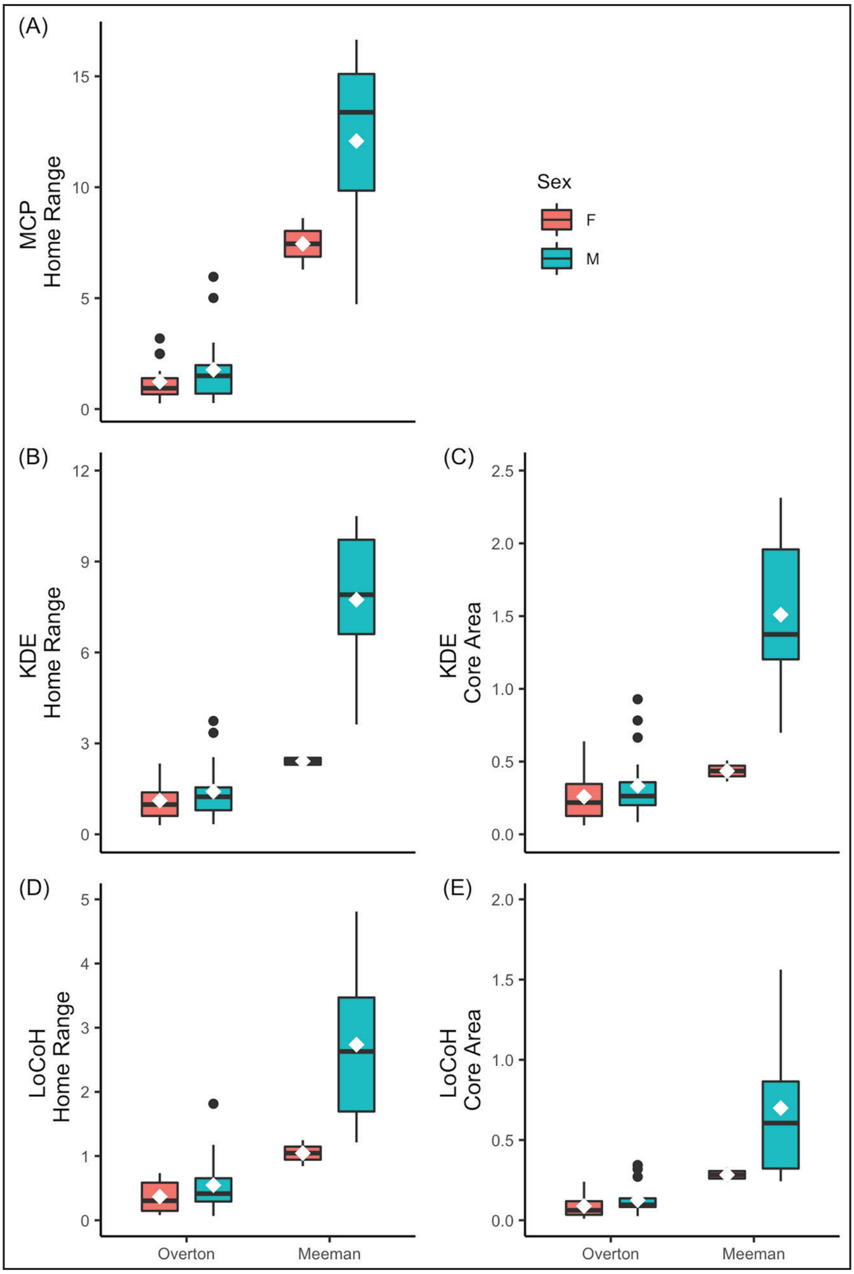

Figure 3. Home range models of Copperhead snakes at urban Overton Park and rural Meeman Biological Station by location and sex. All home range area measurements in hectares. White diamonds denote means. (A) 100% minimum convex polygon (MCP) home range. (B) 95% kernel density estimator (KDE) utilization distribution. (C) 50% KDE utilization distribution. (D) 95% local convex hull (LoCoH) utilization distribution. (E) 50% LoCoH utilization distribution.

Table 3. Results of linear models of home range and core area sizes.

Effect	*F*	df	*P*
MCP			
Sex	2.24	1, 39	0.14
Location	39.6	1, 39	**<0.001**
Year	1.74	2, 39	0.19
KDE 95%			
Sex	3.76	1, 39	0.06
Location	33.8	1, 39	**<0.001**
Year	0.88	2, 38	0.42
KDE 50%			
Sex	4.51	1, 39	**<0.05**
Location	22.7	1, 39	**<0.001**
Year	0.84	2, 39	0.44
LoCoH 95%			
Sex	4.50	1, 39	**<0.05**
Location	21.1	1, 39	**<0.001**
Year	2.35	2, 39	0.11
LoCoH 50%			
Sex	5.39	1, 39	**<0.05**
Location	19.7	1, 39	**<0.001**
Year	2.08	2, 39	0.14

Statistically significant values are indicated in bold.

Table 4. Minimum Convex Polygon (100% MCP) home range models by studies. Mean (SE) expressed in hectares.

Location	Sex	N	MCP
Alabama[A]	M	16	12.0 (1.9)
	F	6	5.6 (1.7)
Connecticut[B]	M	10	17.5 (3.8)
	F	8	5.0 (1.7)
Meeman	M	6	12.1 (1.8)
	F	2	7.4 (1.2)
Nebraska[C]	M	5	9.3 (1.5)
	F	6	2.7 (0.7)
Overton	M	19	1.8 (0.3)
	F	17	1.2 (0.2)

[A] Sutton et al. 2017, [B] Smith et al. 2009, [C] Rodriguez 2010

Movement

We summarized movement by total distance moved, daily movement, and movement per relocation sampling (MPS; Supplemental Table 5, in Supplemental File 1). Non-gravid and gravid females did not differ in total distance moved and were kept as 1 group ($F_{1,\ 17}$ = 3.11, $P = 0.10$). As anticipated, the number of relocations per individual partially explained total distance moved (Table 5). Our analyses found male snakes moved more overall (total distance), per day, and per sampling than female snakes (Fig. 5; Table 5). Rural snakes also generally moved more than urban snakes. We found a year effect on daily movement and MPS. Pairwise comparisons showed a difference in daily movement between all years ($P < 0.05$) and less MPS in 2015 compared to 2016 ($P < 0.05$; other pairwise differences > 0.05). We suggest this finding is probably an artifact of not having subjects from the rural forest during 2015 (Fig. 5).

We analyzed monthly movement by sex, location, and month, controlling for year and individual. Non-gravid and gravid females were kept as 1 group ($F_{1,\ 15}$ = 1.62, $P = 0.22$). We found male individuals moved more than females ($F_{1,\ 37.1}$ = 7.8, $P < 0.01$), and urban snakes moved less than rural snakes per month ($F_{1,\ 35.5}$ = 30.8, $P < 0.001$). The effect of month ($F_{8,\ 289.5}$ = 7.7, $P < 0.001$) and its interaction with sex were also significant ($F_{8,\ 289.8}$ = 2.7, $P < 0.01$). Pairwise comparisons between consecutive months indicated there were significant differences in movement between the months of April–May, May–June, August–September, September–October, and October–November (all pairwise comparisons $P < 0.05$). April–May and August–September are important breeding months for Copperheads in this area. Pairwise comparisons of month and sex suggested that males moved more than females in August and September ($P < 0.05$). We also found a year effect ($F_{2,\ 36.5}$ = 4.2, $P < 0.05$), and pairwise comparisons showed less movement in 2015 compared to 2016 ($P < 0.05$; other pairwise differences > 0.05). We believe this finding is due to the lack of rural snakes during the 2015 season.

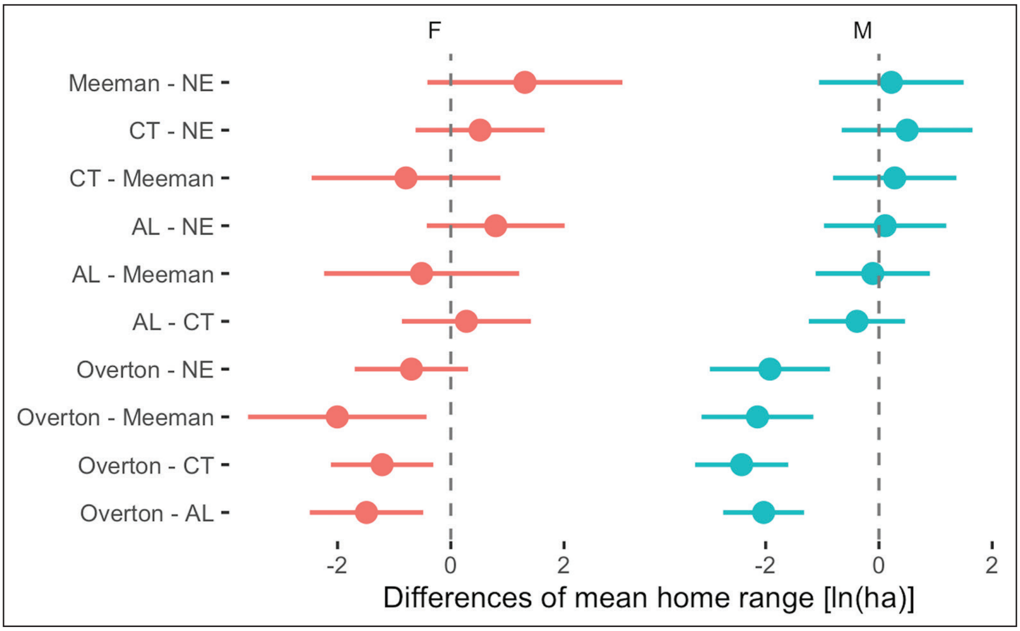

Figure 4. Differences in Copperhead snake mean minimum convex polygon (MCP) home range with 95% confidence intervals by study location (urban Overton Park and rural Meeman Biological Station) and sex. Home ranges were natural log transformed. Rural NE – Nebraska; CT – Connecticut; AL – Alabama.

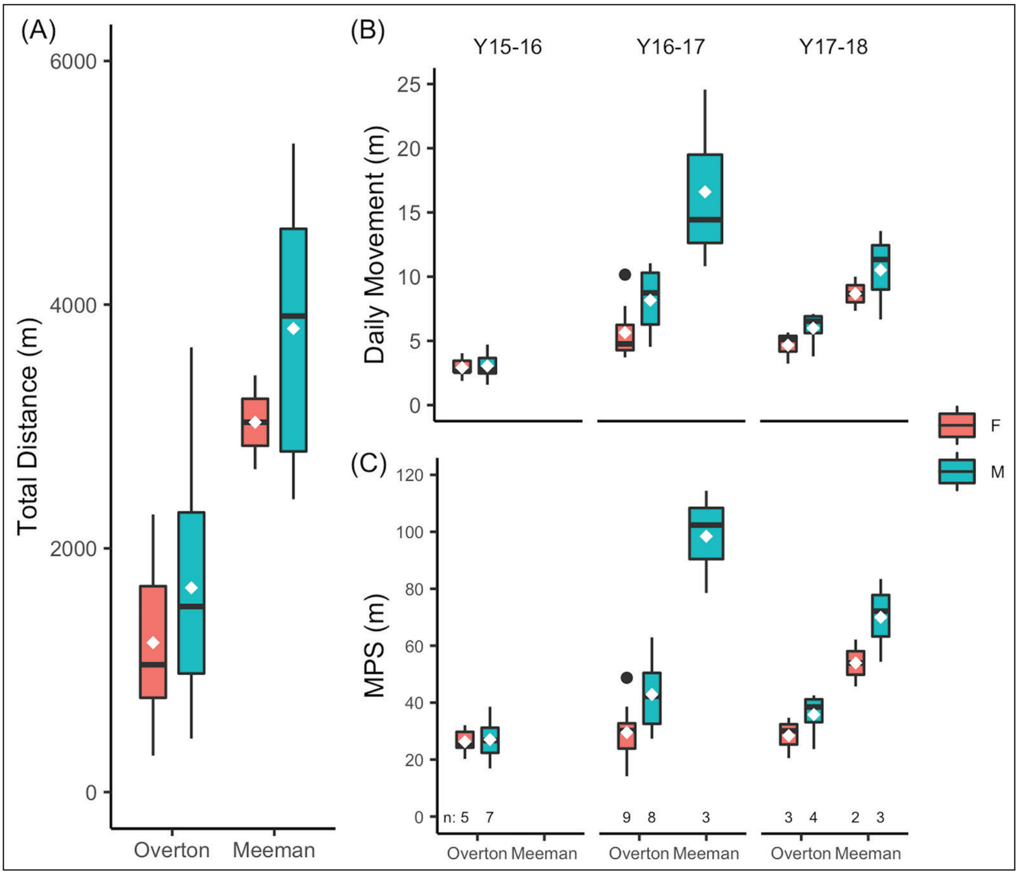

Figure 5. Movement metrics of Copperhead snakes at urban Overton Park and rural Meeman Biological Station by location and sex. White diamonds denote means. (A) Average total distance moved. (B) Average daily movement and (C) average movement per sampling (MPS) also represented by year, as effect was significant.

Table 5. Results of linear models of movement metrics: total distance moved, daily movement, and average movement per sampling.

Effect	*F*	df	*P*
Total Distance			
Number of relocations	89.1	1, 38	**<0.001**
Sex	9.65	1, 38	**<0.01**
Location	51.8	1, 38	**<0.001**
Year	2.88	2, 38	0.07
Daily Movement			
Sex	5.26	1, 39	**<0.05**
Location	21.5	1, 39	**<0.001**
Year	23.3	2, 39	**<0.001**
Movement per Sampling			
Sex	7.87	1, 39	**<0.01**
Location	38.0	1, 39	**<0.001**
Year	3.84	2, 39	**<0.05**

Statistically significant values are indicated in bold.

Discussion

We conducted a longitudinal radio telemetry study comparing the morphology and spatial ecology of Copperhead snakes living within an urban forest fragment and a rural forest. To our knowledge, this is the first detailed radio telemetry study conducted with Copperhead snakes in an urban forest remnant. Because of their widespread distribution, habitat specificity, and observed sensitivity to human disturbance, Copperheads may be a valuable and accessible model reptile species (Caro and O'Doherty 1999). This new understanding of their spatial ecology in an urban forest fragment provides a baseline for future urban reptile studies.

Morphology

We did not find lower body condition (scaled mass index) for snakes in the urban forest compared to those in the rural forest. Body condition is a non-destructive measure of the energy capital of an animal and, therefore, an indicator of health and ability to obtain resources (Peig and Green 2009). Further, body condition is a predictor for reproductive effort in male snakes and ability in females (Aubret et al. 2002, Lind and Beaupre 2015, Lind et al. 2016, Naulleau and Bonnet 1996). We did not find evidence suggesting that the urban Copperheads were experiencing nutritional deficiencies. Some studies have shown decreased body condition in animals living in or near disturbed environments (Lazic et al. 2017, Lomas et al. 2015, Prange et al. 2003). Other studies have shown animals in disturbed areas exhibit similar or increased body condition compared to rural conspecifics, an effect perhaps attributable to resource availability (Bókony et al. 2012, Laverty et al. 2016, Martin et al. 2017, Meillère et al. 2015, Wright and Fokidis 2016). This explanation is likely the case in our research, but it warrants further study on available food sources within the urban site. Broadly, these differences suggest some animals are better able to cope with urban environments, although the nature of the disturbance is not uniform in all urbanization studies (Meillère et al. 2015). However, studies that use condition indices from ordinary least-squares residuals may not be as reliable as those using scaled mass indices (Peig and Green 2010). In fact, results can be contradictory within the same dataset depending on index (Bókony et al. 2012, Liker et al. 2008), confounding generalizations about the effects of urban disturbance when body conditions are measured using different metrics. Multiple behavioral and physiological metrics are important to develop a holistic understanding of the organism.

Although the relative ratio between mass and length (SVL) did not differ between the Copperhead populations, we did find the urban snakes were smaller in both of those metrics. Previous studies have shown urban animals tend to be smaller than their non-urban counterparts (Lomas et al. 2015, Wolfe et al. 2018a), with some exhibiting no difference in body condition (Bókony et al. 2012, Meillère et al. 2015). In vipers, body length is a predictor for male reproductive success (Levine et al. 2015, Schuett 1997) and for female reproductive maturity and litter size (Ernst 1992, Holycross and Goldberg 2006, Lind et al. 2016). Copperheads are viviparous, and fat storage and length (SVL) are important indicators of frequency of female reproduction (Aubret et al. 2002, Fitch 2003, Holycross and Goldberg 2006). Hence, smaller body size could decrease lifetime reproductive ability (Halliday and Verrell 1988) and should be investigated in future urban population studies.

There are several potential, non-mutually exclusive explanations for why our urban snakes were smaller than rural conspecifics. First, diets may differ between the populations. Copperheads are generalists and will eat a variety of animals, including ecto- and endothermic prey (Ernst and Ernst 2011). The Copperheads at our locations may have different available prey (Fischer et al. 2012) or feed at different frequencies (Wolfe et al. 2018a). Furthermore, Copperheads at the urban forest may not grow as quickly as their rural counterparts (Hokit and Branch 2003, Moreno-Arias and Urbina-Cardona 2013), or population demographics may be skewed toward younger age classes (Holland and Bennett 2010). Without extensive survey work of animals followed since birth, it is difficult to determine if the urban population is composed of younger snakes (Halliday and Verrell 1988). Finally, genetic differences between the populations may be a contributing factor. In a concurrent study, we found evidence for lower genetic diversity within the urban population (Carrasco-Harris et al. 2020). Future work may consider the relationship between genetic diversity and fitness metrics in urban populations (Szulkin et al. 2010)._

Spatial Analyses

We found snakes at the urban forest had smaller home ranges and core areas than those from the rural forest, as well as other previously studied populations of Copperheads. Further, urban snakes moved less in all movement metrics compared to rural snakes. One possibility is that snakes in the urban forest (57 ha) had smaller home ranges than snakes in the rural forest (252 ha) because there is less area in which to have a typical home range. However, the MCPs of Meeman rural snakes ranged from 4.7–16.7 ha. The urban home range could have been as large as that of a rural snake and still fit within the suitable habitat of Overton. This finding suggests the urban snakes may modify spatial behavior in this forest, tolerating human disturbances to succeed in this environment (Lowry et al. 2013). Sex-based differences for home ranges and movement patterns were anticipated (Smith et al. 2009, Sutton et al. 2017), although the differences between males and female were less pronounced at the urban forest. Seasonal changes in activity in the spring and late summer were also expected, as it has been previously noted that southeastern Copperheads mate twice a year (Aldridge and Duvall 2002, Ernst and Ernst 2011). Urban subjects may have smaller home ranges and core areas because of denser food availability (Wasko and Sasa 2012), predator release (Steen et al. 2014), human disturbance (Beale et al. 2016), or a combination of circumstances.

Our results align with other studies in disturbed or fragmented environments. Studies have shown snakes adjust to human disturbance by altering movement patterns and remaining concealed more frequently (Beale et al. 2016, Lomas et al. 2019, Pattishall and Cundall 2008). Others have shown snakes decrease home range size in fragmented areas, including those that interface with human development (Breininger et al. 2011, Mitrovich et al. 2009). In contrast, some snakes and other reptiles do not exhibit movement differences in smaller fragments surrounded by urban areas, in particular if these fragments meet the minimum size required for persistence, the species is not territorial, or the animal is able to use urban or edge habitats (Anguiano and Diffendorfer 2015, Kwiatkowski et al. 2008, Row et al. 2012). These findings suggest that some urban-persisting reptiles with limited dispersal capacity exhibit behavioral plasticity in modified environments and others may not. Although a translocation study would be useful to test behavioral plasticity, translocated snakes often increase movement compared to residents and may have greater mortality (Wolfe et al. 2018b). Further research should investigate the costs and benefits of plasticity in animals that persist within or near the urban interface (French et al. 2018, Lomas et al. 2015, Mitchell 1998).

Limitations

Some limitations of our study are having a smaller sample size at the rural forest than at the urban forest and having only 2 years of data for rural snakes compared to 3 years for urban snakes. Movement differences by year were most likely an artifact of the addition of the rural site in 2016. Because of the cryptic nature of Copperheads, we had difficulty finding suitable adults at this location. When tracking in the urban forest, it was not uncommon to find adult conspecifics near the focal subject. At our rural site, focal males were found primarily during the spring breeding season. During the summer, males were tracked in a field of native *Ambrosia trifida* Linnaeus (Giant Ragweed) and invasive *Pueraria montana* (Loureiro) Merrill (Kudzu), and a trail system had to be blazed to triangulate the animals during relocations. It was very unlikely we were going to capture new snakes in these conditions. Unequal sample sizes are often unavoidable in observational ecological studies.

Differences by sex depended on the model, but there are limitations in these comparisons because of the small female sample size at the rural forest. Differences by reproductive status have been previously noted but were not found to be significant in our study. First, the limited sample size of females at the rural forest (1 gravid, 1 non-gravid at capture) hindered our ability to determine if differences exist between reproductive and non-reproductive females within and between locations. Further, reproductive females may have been falsely identified as non-gravid if caught early in the season. Checking reproductive status by palpating would mean regular handling of all snakes. We avoided intrusive handling that may have led to physiological responses (Bailey et al. 2009, Schuett et al. 2004) and potential behavior changes in focal subjects. After transmitter implantation, animals were only captured to remove the transmitter or if there was an apparent medical reason related to the surgery (Supplemental Table 2, in Supplemental File 1).

We acknowledge the study is limited by having 1 urban forest and 1 rural comparison site with fewer individuals. If resources permit, research on the relationship between urbanization and behavior should include more urban forests, allowing for greater generalizations. However, urban forests may differ in degree of recreational usage and trails, fragment size, surrounding urbanization density, and climate zones. Studies that include multiple urban sites should standardize for location differences and acknowledge each fragment's unique characteristics (Moll et al. 2019). Our results should be taken as a case study and in consideration with previous research on urban snake populations.

Conclusions

Our study provides detailed analysis of the morphology and spatial ecology of a persisting Copperhead population isolated in an urban forest fragment. As urbanization continues, it is likely that natural areas will become surrounded by development and possibly set aside for human recreation. Natural areas that maintain structural complexity harbor native reptiles that would otherwise be excluded from the urban matrix (Alvey 2006, Hamer and McDonnell 2010, Harden et al. 2009, Vanegas-Guerrero et al. 2016). Research aimed at understanding urban forests is important for understanding how animals in these fragments persist and how land managers can best maintain habitats for both human recreation and biodiversity (Bonnet et al. 2016, Garden et al. 2010).

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