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Urban Land Cover Associated with Space Use in Woodland Box Turtles (*Terrapene carolina carolina*)

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***Abstract.*—Many bird and mammal taxa exhibit a decrease in the size of their space use area in response to urban land cover; however, few studies have assessed whether urban land cover drives disruption in space use in less mobile and physiologically disparate taxa, such as reptiles. To determine how urban land cover impacts space use in Woodland Box Turtles (*Terrapene carolina carolina*), we quantified land cover variables (forest, road density, and impervious surface) at three spatial extents (250-, 500-, and 1500-m radii) along a gradient of urban land cover and related these variables to box turtle space use metrics in the rapidly urbanizing Piedmont region of South Carolina. In females, the best supported models showed that average pairwise distance and 100% Minimum Convex Polygons decreased with increasing impervious surface and decreasing forest. In males, there was little or no relationship between space use area and land cover, suggesting that females may be particularly sensitive to urban land cover. The observed relationship was only evident at the 500-m radius, suggesting that the forest patch size and the urban land cover in the immediate surroundings are important drivers of reduced space use. Thus, we demonstrated that the pattern of movement disruption occurring in birds and mammals also occurs in a reptile, but the response to urban land cover can be sex specific. Reduced vagility may affect population persistence by reducing female fitness, gene flow, and demographic exchange. Preservation and restoration of large habitat patches and establishment of corridors between isolated habitat patches are likely needed to prevent space use change and its negative consequences.**

Key Words.—forest loss; land cover change; home range; movement ecology; Piedmont; reptile; urbanization

Introduction

Human land use and activities now permeate more than three quarters of the ice-free surface of the Earth, dramatically changing land cover and encroaching on wildlife habitats (Ellis et al. 2010; Venter et al. 2016). These anthropogenic changes are driving widespread shifts in wildlife movement behavior (Doherty et al. 2021). Because animal movement mediates individual fitness (Andreassen and Ims 1998), gene flow (Banks and Lindenmayer 2014), and metapopulation dynamics (Muths et al. 2018), disruption in movement can have profound impacts on population persistence. Therefore, understanding how humans drive changes in the movement of individual animals can help in developing targeted conservation strategies (Allen and Singh 2016; Doherty and Driscoll 2018).

Urbanization, the process by which natural or rural land cover is replaced by impervious surface, is recognized as a major threat to wildlife populations. Urbanization creates novel environments that influence the movement and space use of wildlife. Urbanization typically reduces habitat patch size and intersperses habitat patches with urban infrastructures such as roads, buildings, paved areas, and other impervious surfaces. Pervasive impervious surface cover can act as a physical or perceived barrier to animal movement (Shepard et al. 2008). Urbanization also alters the abiotic (temperature, substrates, hydrology) and biotic (vegetation, invasive species, urban-subsidized predators) conditions in the habitat patch, thus altering the distributions of the resources and risks that determine animal movement and space use (Doherty et al. 2019; Carrasco-Harris et al. 2020). Furthermore, urban areas undergo anthropogenic disturbances such as vehicle traffic and frequent presence of people and pets, which can drive behavioral changes in wildlife (Ciuti et al. 2012; Doherty et al. 2017; Greenspan et al. 2018) and often lead to death (Brisbin et al. 2008; Nazdrowicz et al. 2008).

Studies of urban impacts on wildlife movement and space use have increased in the last three decades. A recent meta-analysis on three vertebrate taxa representing 32 species revealed that 88% of the 41 comparisons exhibited reduced space use (O'Donnell and Delbarco-Trillo 2020); however, this pattern is largely based on birds and mammals. Reduced space use was also noted for reptiles, but this pattern was not conclusive due to a paucity of studies on reptiles. Because reptiles are ectothermic and less mobile than mammals and birds (Todd and Nowakowski 2021), they may be more sensitive than mammals and birds to land cover change. Therefore, we expect reptile space use to also be smaller in response to urban land cover.

Woodland Box Turtles range throughout the eastern U.S. and primarily inhabit hardwood and pine forests (Kapfer et al. 2013; Kiester and Willey 2015). Woodland Box Turtles are omnivores and eat a wide variety of invertebrates and plant matter including fruits (Dodd 2001). Movement rates generally increase during mating season in males and nesting season in females; however, space use areas of females are larger than those of males (Habeck et al. 2019; Roe et al. 2020). Woodland Box Turtles are long-lived and reproduce multiple times throughout their lifespan. Females typically nest in open canopy habitat (Congello 1978; Willey and Sievert 2012; Refsnider et al. 2022). The long distances females travel to suitable nest sites is thought to explain why female space use area tends to be larger than that of males (Habeck et al. 2019; Roe et al. 2021).

Herein, we report the effects of urban land cover on the space use of a threatened reptile, the Woodland Box Turtle (*Terrapene carolina carolina*). Woodland Box Turtles have declined throughout their range over the last several decades and are classified as Vulnerable by the International Union for Conservation of Nature (van Dijk 2011). Increasing evidence suggests that urbanization is associated with reduced abundances of Woodland Box Turtles (Budischak et al. 2006; Roe et al. 2021; Graham et al. 2022). To determine whether urbanization affects box turtle space use, we quantified the space use of male and female box turtles along a gradient of urban land cover (decreasing forest extent, increasing road density, and increasing impervious surface) measured at three spatial extents (250-, 500-, and 1500-m radii).

Materials and Methods

Study area.—This study was conducted in the Piedmont ecoregion in South Carolina, USA. This region is undergoing rapid urbanization and forest loss, with 75% of the newly developed land between 1950 and 2000 coming from forests (Brown et al. 2005). Since 1973, the Piedmont has experienced a net 4.8% decrease in forest cover (Brown et al. 2005; Drummond and Loveland 2010). Urban land cover in the Piedmont is predicted to expand by 165% by 2060, the largest absolute change in land cover in the southeastern U.S. (Terando et al. 2014). Historically, this region consisted of old-growth forests comprised of oak (*Quercus* spp.), hickory (*Carya* spp.), and pine (*Pinus* spp.). After the arrival of Europeans, most of the land cover was converted to farmland, which was eventually abandoned and became secondary-growth oak and pine forests. In recent decades, the region has rapidly urbanized, with most of the newly developed land resulting from the loss of these secondary-growth forests (Brown et al. 2005).

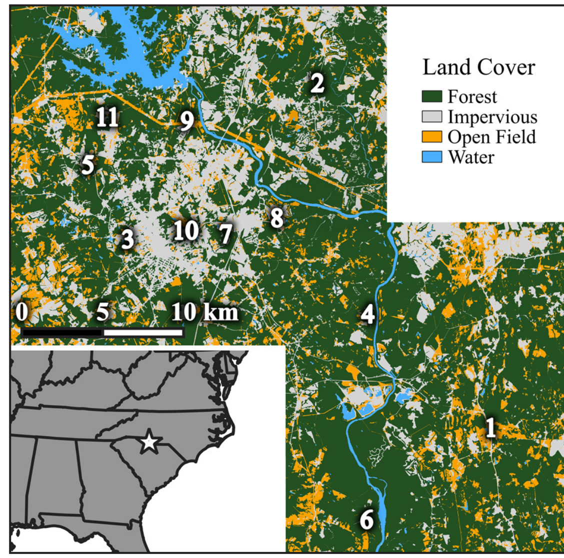

Figure 1. Distribution of sampling sites (numbers) along gradients of urban intensity in northcentral South Carolina, USA (inset, lower left). Land cover is classified from aerial imagery (https://www.usgs.gov/centers/eros/science/usgs-eros-archive-aerial-photography-national-agriculture-imagery-program-naip) using the Semi-Automatic Classification Plugin for QGIS (Congedo 2021).

We established 11 sampling sites along a gradient of urban land cover around the city of Rock Hill, South Carolina (Fig. 1). We do not provide exact locations to avoid encouraging people to collect turtles from these sites. Rock Hill is currently undergoing rapid development as part of the urban sprawl of the nearby city of Charlotte, North Carolina, USA. The size of the human population in Rock Hill was estimated to be 75,048 people in 2019 (https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html). Sampling sites ranged in size from small city parks to large state parks. Overstory vegetation in all sampling sites was mostly composed of native conifer and hardwood species. Understory vegetation in urban sites was dominated by non-native species, mainly Autumn Olive (*Elaeagnus umbellata*), Japanese Stiltgrass (*Microstegium* *vimineum*), and Chinese Privet (*Ligustrum sinense*). Land cover surrounding the forests at urban sites consisted of mainly residential and commercial buildings, streets, and other pavement, but also lawns and open fields interspersed with patches of early successional plants such as honeysuckle (*Lonicera* spp.), blackberry (*Rubus* spp.), and grasses. To reduce potential influences of environmental gradients unrelated to urbanization, we established sampling sites in different directions from the center of the city. To minimize potentially confounding effects of other habitat characteristics apart from the land cover gradient, all sampling sites were selected in secondary growth forests, with at least one stream or water body within the forest. We chose sites before knowing the presence or absence of turtles, but no sites completely lacked turtles.

Radio telemetry.—From April through early November in both 2018 and 2019, we conducted visual surveys to capture box turtles to which we attached radio transmitters. Upon capture, we recorded the location with a handheld GPS unit (GPSMAP 64s or 64sc, Garmin Ltd, Schaffhausen, Switzerland). We determined the sex of each turtle by morphological features including distance from the cloaca to the tip of the tail, concavity of the plastron, length of the claws, and coloration (Nichols 1939; Stickel and Bunck 1989; Graeter et al. 2013). We did not assess gravidity.

We affixed a radio transmitter (RI-2B, Holohil Systems Ltd., Ontario, Canada; or A2400, Advanced Telemetry Systems, Isanti, Minnesota, USA) using PC-7 two-part epoxy to the carapace on the lower posterior side so as not to interfere with mounting during mating. We used transmitters that were < 5% of the body mass of the individual to avoid impeding the activity of the turtle. We avoided covering the growth zones between the scutes with the transmitter or epoxy. We kept the turtles overnight until the epoxy hardened and released them at their original point of capture the next day. We used a handheld radio receiver (ATS R410) with a three-element folding Yagi antenna (both from Advanced Telemetry Systems) and we tracked each turtle once every other week on average, from 1 April to 27 November in 2018, from 12 April to 20 December in 2019, and from 8 January to 8 March in 2020. For each detection, we recorded the land cover on which the turtle was found (Fig. 2).

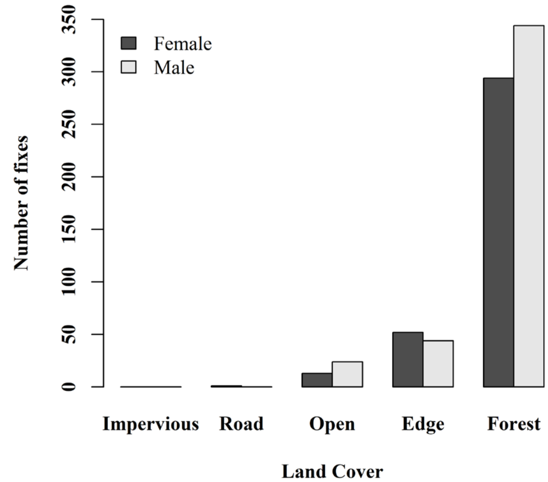

Figure 2. Detected locations of either sex of Woodland Box Turtle (*Terrapene carolina carolina*) by land cover type. Impervious is a non-road impervious surface; Road is a paved street or highway; Open is a field or bare ground without canopy cover; Edge is an area within 6 m of forest boundary inside of the tree line; and Forest is an interior forest (areas at least 6 m into the forest interior).

Quantification of land cover.—Using the supervised interactive classification tool in QGIS, we classified the land cover into the following categories: (1) forest; (2) impervious surface; (3) open (field or bare ground); and (4) water from high-resolution (1 m) 2019 National Agricultural Imagery Program aerial imagery (https://www.usgs.gov/centers/eros/science/usgs-eros-archive-aerial-photography-national-agriculture-imagery-program-naip). Land cover was classified at three different radii (250 m, 500 m, and 1,500 m) around the centroid of all detection locations for each turtle (Fig. 3, Supplemental Information Tables S1-S2). We quantified road density within each of the radii using 2019 TIGER/Line shapefiles (https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html) by dividing the total length of roads (m) by the area of the circle (m2; Supplemental Information Tables S1-S2). We did not quantify intensity of road use or traffic speeds because these data were not readily accessible for all road types in our study area. The 250 m radius for each turtle included most of its detected locations and represents the estimated central area of activity of an individual. The 500 m radius for each turtle included the entirety of its 100% Minimum Convex Polygon (MCP), which contains all detection locations obtained for an individual (Mohr 1947), and some of the surrounding landscape matrix, which should represent potential effects on movement at the habitat

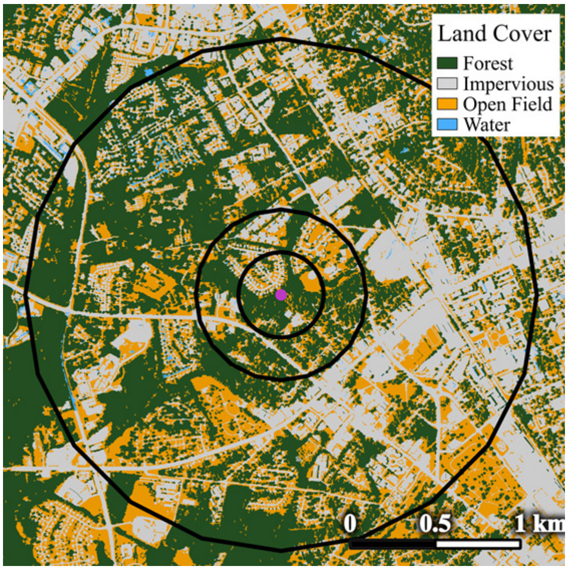

Figure 3. Example of land cover quantified at three spatial extents around the centroid (purple) of detection locations for an individual Woodland Box Turtle (*Terrapene carolina carolina*). Innermost circle = 250-m radius, middle circle = 500-m radius, outermost circle = 1,500-m radius. Land cover is classified from aerial imagery (https://www.usgs.gov/centers/eros/science/usgs-eros-archive-aerial-photography-national-agriculture-imagery-program-naip) using the Semi-Automatic Classification Plugin for QGIS (Congedo 2021).

patch level. We chose the 1,500 m radius to account for potential long-range movements within or among fragmented forest patches (e.g., Blake et al. 2023).

Space use area.—We estimated space use area using 100% MCP (Fig. 3). MCP is prone to variation in the number of locations and duration of tracking among individuals. To account for variation in sampling among sites, we also calculated the average distance between all pairs of detection locations (AD). This distance metric is strongly positively correlated with MCP and does not vary with the number of detection locations (Püttker et al. 2012). We calculated MCP and AD using the adehabitatLT package in R (Calenge 2006).

Analysis.—Urbanization is often quantified with the extent of forest, impervious surface, and roads (McDonnell and Hahs 2008; Van de Voorde et al. 2011; Terando et al. 2014). Accordingly, we used only these land cover classes to assess the effects of urban land cover on space use metrics. Because the forest and impervious surface land cover may have joint effects on box turtle space use, we performed a Principal Component Analysis (PCA) for forest and impervious surface area to create a composite variable as the first principal component (PC1).

We assessed the effects of land cover on the space use of a turtle using Linear Mixed-effects Quantile Regressions (Geraci 2014; Geraci and Bottai 2014). We modeled an upper quantile (75%) in response variables because we were interested in whether urbanization imposed an upper limit on space use. Models were constructed separately for either response variable (MCP and AD) with a single predictor (forest, impervious surface, road density, or PC1) at each spatial extent as the fixed effect and the sampling site as the random effect. We standardized all predictors to have a mean of zero and a standard deviation of one so that their regression coefficients from variables with different units and magnitude could be meaningfully compared. We only used one fixed effect in each model to avoid overfitting because our sample size was small. We analyzed females and males separately to account for potential sex difference in their responses. We assessed the relative importance of models for each response variable using the Akaike Information Criterion corrected for small sample sizes (AICC). All statistical analyses were conducted using R version 4.0.3.9 (R Development Core Team 2019).

Results

Higher PC scores reflected increasing area of forest and decreasing area of impervious surface. For females, PC1 accounted for 88.5%, 89.8%, and 95.2% of variation in the landcover dataset at the 250, 500, and 1,500 m radius, respectively. For males, PC1 accounted for PC1 92.1% for the 250-radius, and 94.4% of variation in the landcover dataset at both the 500- and 1,500-m radii. Variable loadings varied from 0.94 to -0.97 (Table 1).We tracked 96 adult box turtles: carapace length of females (mean ± standard deviation) was 12.0 ± 0.97 cm and for males was 13.1 ± 0.80 cm. We tracked an average of 3.8 ± 1.89 females and 4.7 ± 1.89 males per site and obtained an average of 8.7 ± 2.48 relocations per turtle (median = 9 for both females and males). The average total time from first finding an individual to the end of tracking was 420.2 ± 131.16 d (median = 449 for females and 444 for males). We included only the turtles for whom we had at least five detections in our analysis (42 females and 46 males). There was no practical difference between sexes in land cover used (Fig. 2). Both sexes were located predominantly in forest compared to other land cover types. Four individuals (two females, two males) crossed rural roads, one female was detected once on

Table 1. Loadings of land cover classes from a Principal Component Analysis to create a composite variable (first principal component) representing the joint effect of forest and impervious surface on space use of either sex of Woodland Box Turtle (Terrapene carolina carolina). Composite variables were created for land cover quantified at three spatial extents (radii) from the centroid of detection locations for each turtle.

Sex	Radius (m)	Land Cover	Loading
Female	250	Forest	-0.94
		Impervious	0.94
	500	Forest	0.95
		Impervious	-0.95
	1,500	Forest	0.98
		Impervious	-0.98
Male	250	Forest	-0.93
		Impervious	0.93
	500	Forest	-0.96
		Impervious	0.96
	1,500	Forest	-0.97
		Impervious	0.97

a small residential road, and no telemetered turtles crossed highways or urban or suburban streets. We did not detect any telemetered turtles on other types of impervious surface. Fewer than 6% of detections occurred in open area, which consisted of any non-impervious surface outside of the forest such as fields or lawns. We found one female once digging a nest under a canopy opening within the forest.

Table 2. Sample size (n), mean (x̄), and standard deviation (SD) of space use metrics quantified for each female Woodland Box Turtle (*Terrapene carolina carolina*) at 11 sites in northcentral South Carolina, USA. Space use metrics are 100% Minimum Convex Polygons (MCP) and average pairwise distance between radio telemetry detected locations (AD) for each turtle.

		MCP (ha)		AD (m)	
Site	n	x̄	SD	x̄	SD
1	3	3.27	2.81	116.96	55.55
2	7	2.46	1.93	153.45	67.57
3	1	0.04		47.42	
4	4	1.08	1.39	87.13	42.63
5	4	1.08	1.05	94.14	50.23
6	5	5.61	5.74	167.39	119.47
7	3	0.13	0.07	39.21	13.53
8	3	0.67	0.78	59.14	26.47
9	3	3.48	5.44	184.37	242.96
10	7	1.47	1.12	95.07	34.79
11	2	1.00	0.27	85.68	8.54

Table 3. Sample size (n), mean (x̄), and standard deviation (SD) of space use metrics quantified for each male Woodland Box Turtle (*Terrapene carolina carolina*) at 11 sites in northcentral South Carolina, USA. Space use metrics are 100% Minimum Convex Polygons (MCP) and average pairwise distance between radio telemetry detected locations (AD) for each turtle.

		MCP (ha)		AD (m)	
Site	n	x̄	SD	x̄	SD
1	7	0.62	0.27	80.26	25.52
2	4	1.46	1.44	97.89	50.18
3	0				
4	7	0.73	0.62	71.65	51.07
5	7	1.42	1.11	87.27	34.48
6	3	1.23	0.41	107.37	34.24
7	5	0.49	0.43	107.74	44.08
8	3	0.32	0.35	55.52	38.38
9	3	0.19	0.04	42.40	6.23
10	2	0.41	0.32	55.53	33.80
11	5	0.61	0.44	67.99	19.82

Home range and space use.—Overall, female space use was larger than that of males (Tables 2–3); mean MCP of females (2.1 ± 2.94 ha) was 2.6 times larger than that of males (0.8 ± 0.77 ha), and the 0.75 quantile of MCP of females (3.1 ha) was 2.8 times larger than that of males (1.1 ha). The observed MCPs covered only a small fraction of the entire extent of the forest patch at any of the sampling sites; however, MCPs often extended to forest edges (or land cover immediately outside the forest) that were bordered by open fields, roads, or other impervious surfaces (Fig. 4). The mean percentage of available forest in a 500-m radius occupied by MCPs was 3.43% ± 4.40% for females and 1.61% ± 1.72% for males.

In females, the model with forest cover within a 500-m radius was best supported by the data (ΔAICC = 0). The second-best supported model was the one with PC1 of forest cover and impervious surface cover within a 500-m radius (ΔAICC = 1.1; Fig. 5, Supplemental Information Table S3). The best model was about twice as likely as the second-best model, which, in turn, was 3.8 times more likely than the third best-supported model that included the PC1 of forest and impervious surface at the 1500-m radius (ΔAICC = 3.7; Supplemental Information Table S3). On the other hand, in males, no model performed

Figure 4. Examples of space use (100% Minimum Convex Polygon; MCP) of male (white, hatched) and female (blue, cross-hatched) Woodland Box Turtle (*Terrapene carolina carolina*) at our study site in northcentral South Carolina, USA. Each polygon represents one turtle. (A) MCPs of three female and seven male turtles in a non-urban site with a large forest patch. (B) MCPs of three female and four male turtles in an urban site with a small forest patch. Both A and B feature aerial imagery (https://www.usgs.gov/centers/eros/science/usgs-eros-archive-aerial-photography-national-agriculture-imagery-program-naip).

better than the intercept-only model for MCP (Fig. 5, Supplemental Information Table S4). Consistent with the sex difference in MCP, females exhibited larger values for AD than males (Tables 2–3); the mean AD of females (112.4 ± 86.89 m) was 1.5 times larger than that of males (79.8 ± 38.38 m), and the 0.75 quantile of AD of females (140.6 m) was 1.4 times that of males (100.0 m). In females, the models with forest cover within a 500-m radius was best supported by the data (ΔAICC = 0; Fig. 6, Supplemental Information Table S5). The model with PC1 of forest cover and impervious surface cover within a 500-m radius was nearly equally supported (ΔAICC = 0.06; Fig. 6, Supplemental Information Table S5). These two best models were 5.4 times more likely than the next-best supported model that included impervious surface cover within a 500-m radius (ΔAICC = 3.4; Supplemental Information Table S5). The largest value for female AD predicted by the best model was eight times larger than the smallest value predicted. In males, impervious surface cover at the 1,500-m scale and at the 500-m scale were the only models for AD which performed better than the intercept-only model (Fig. 6, Supplemental Information Table S6); however, these models had low weights and confidence intervals including zero.

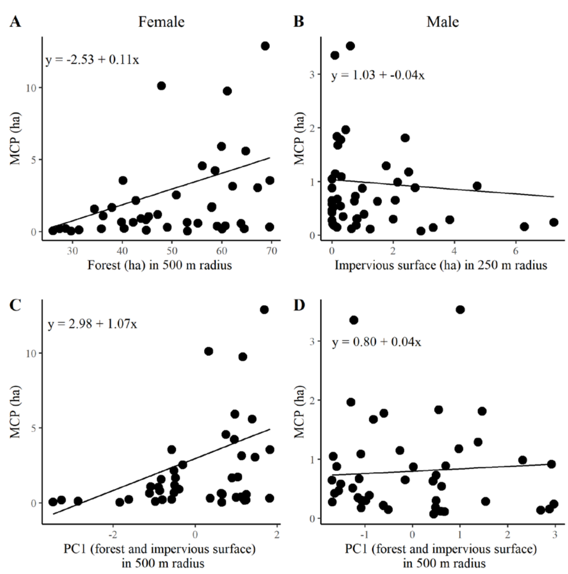

Figure 5. Relationships between size of 100% Minimum Convex Polygons (MCP) and land cover depicted by linear quantile (0.75) mixed models for female (left column) and male (right column) Woodland Box Turtles (Terrapene carolina carolina). For females, the two best supported models based on AICC are presented here. For males, the best supported model was the intercept-only model, so the second and third best supported models are presented here. PC1 is the first principal component derived from Principal Component Analysis of forest and impervious surface area.

Discussion

Overall, space use declined with decreasing forest and increasing impervious surface area in females. The apparent lack of relationships between male space use and measured land cover implies that effects of urban land cover on space use is sex specific. The

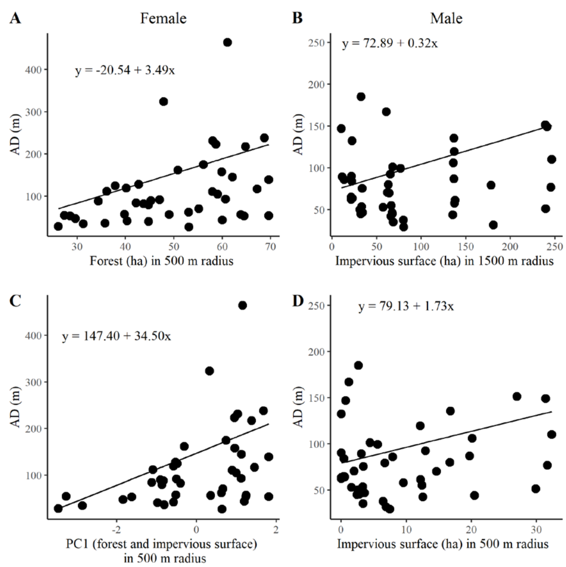

Figure 6. Relationships between average pairwise distance among all detection locations (AD) and land cover depicted by linear quantile (0.75) mixed models for female (left column) and male (right column) Woodland Box Turtles (*Terrapene carolina carolina*). The two best supported models based on Akaike Information Criterion corrected for small sample sizes are presented here. PC1 is the first principal component derived from principal component analysis of forest and impervious surface area.

relationship between land cover variables and space use metrics was only evident at the 500 m radius. For each turtle, the 500 m radius in urban areas contained the entire 100% MCP plus land cover immediately surrounding the forest patch, suggesting that the size of the forest patch and the extent of impervious surface in the immediate surroundings impose an upper limit on their space use area.

Our observed decline in box turtle space use with increasing urban land cover is consistent with reports from previous studies on reptiles. A single site study on Woodland Box Turtles found that movements were confined within a small, isolated urban forest patch (Iglay et al. 2007), and another study comparing one urban park to one rural forest patch found that Three-toed Box Turtles (*T. c. triunguis*) in the rural forest had larger home ranges than those in the urban park (Blake et al. 2023). A summary of box turtle home range literature shows small home range sizes in smaller forest fragments regardless of disturbance type, although no statistical comparison was made (Currylow et al. 2012). Multiple species of snakes were also observed to exhibit reduced space use in urban habitats (Mitrovich et al. 2009; Bauder et al. 2020; Carrasco-Harris et al. 2020; Maddalena et al. 2020). As is common in ecological studies, however, previous studies lack within-study replications (multiple treatments and controls), so the apparent effect cannot be unambiguously linked to the treatment (Oksanen 2001). Using an urban-nonurban gradient (with multiple urban and nonurban sites), our study provides a compelling case study for reduced space use attributable to urban land cover in a reptile. Observed reduction in space use in our study is consistent with the pattern observed in the more mobile, physiologically disparate birds and mammals (O'Donnell and Delbarco-Trillo 2020).

Urban resource subsidies or concentration of resources into smaller areas may drive reduced space use (Fuirst et al. 2018; O'Donnell and Delbarco-Trillo 2020). Urban forest patches typically have large proportions of edge and early successional habitats (Zipperer and Guntenspergen 2009). These habitats may provide a broader thermal gradient within smaller areas (Currylow et al. 2012). Females require open or edge habitat with higher temperatures for nesting (Wilson and Ernst 2008; Fredericksen 2014). Availability of thermally suitable sites in proximity would eliminate the need for long distance nesting forays, reducing space use area for females. On the other hand, male space use during the active season mainly involves searching for mates and would not be influenced by nest site availability. This difference between the sexes in the behavior driving their space use during the active season may explain why females had reduced space use with more urban land cover, while male space use had no relationship to land cover.

Forest edges and early successional habitats also encourage herbaceous and shrub species that provide abundant food. For example, urban forests in our study area are typically dominated by nonnative Autumn Olives (*Elaeagnus umbellata*; pers. obs.), which is a potential food item of box turtles (Weiss 2009; pers. obs.). Blackberries (*Rubus argutus*), dewberries (*Rubus flagellaris*), and Indian Strawberries (*Potentilla indica*), which are common food items of box turtles (Klimstra and Newsome 1960; Figueras et al. 2021), are also abundant (pers. obs.). In most reptiles, females have higher energetic demands for reproduction and rely on energy stored in the previous year or years for reproduction (Bonnet et al. 1998; Shine 2005). A high energy demand by females may make females more responsive to changes in resource availability associated with urban land cover.

Reduced space use area in urban areas may also result from avoidance of urban features. Estimated space use areas were often bordered by impervious surfaces, indicating that box turtles are exposed to urban land cover. Animals may avoid impervious surface (e.g., parking lots, buildings, and roads) because it lacks essential resources, presents unfavorable microclimates, or risks of injuries and mortalities (Sears et al. 2016). Woodland Box Turtles are known to avoid roads (Shepard et al. 2008; Weigand et al. 2019). The avoidance of impervious surfaces may be driven by actual or perceived risks from people and other predators common in urban areas, such as Domestic Dogs (*Canis familaris*) and Northern Raccoons (*Procyon lotor*; Prange et al. 2003; Greenspan et al. 2018). In our study area, females tended to have larger space use area than males, likely due to their nesting forays (Habeck et al. 2019; Roe et al. 2020). Long-distance movements such as nesting forays may be impeded by these urban structures.

A reduction in space use area in urban habitat may result also from avoidance of conspecifics in small habitat patches (Mitrovich et al. 2009). Box turtles are not territorial (Stickel 1950); however, males can show aggression to each other (Roe et al. 2020). Aggression between males would be expected to drive reduced space use area in males in small urban forests. The apparent lack of relationship between urban land cover and male space use area suggests that avoidance of conspecifics does not explain why only females exhibited reduced space use in this study.

Alternatively, reduced space use area in urban habitats may not be a result of behavioral alterations but as a result of loss of individuals with large space use areas from small urban habitat patches. Animal movement is at least partially driven by heritable personality traits (Dingemanse et al. 2002; Cote et al. 2010; Bailey et al. 2021). Bolder individuals may move farther, seeking better foraging or nesting grounds (Chapman et al. 2011; Seltmann et al. 2014) and may thus emigrate from small urban habitat patches. Such individuals may not only leave small habitat patches, but also incur high mortality from anthropogenic factors, such as mowing, motor vehicle strikes, predation, or collection by people (Brisbin et al. 2008).

In conclusion, female Woodland Box Turtles demonstrated reduced space use in urban areas. Our results suggest that the size of forest patches and the prevalence of urban land cover in the immediate surroundings impose an upper limit on the extent of their space use. Likely drivers of reduced space use include urban resource subsidies, avoidance of urban features, or the selective loss of individuals with large space use. Although the underlying mechanisms of space use reduction are unclear, reduced vagility can have negative consequences for population persistence through reduced gene flow and demographic exchange, thereby influencing genetic variation and metapopulation dynamics. Accordingly, protecting Woodland Box Turtles in urban landscapes requires establishment of corridors or stepping-stone habitat patches (such as conversion of lawns to more natural prairie communities) and the protection or restoration of the remaining forest areas.

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