EVALUATING PREDATOR-PREY DYNAMICS IN AN URBAN FOREST: ASSESSMENT USING RAPTOR PREDATION ON PREY MIMICS

by

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INTRODUCTION

Urbanization has resulted in changes in ecological functions and trophic interactions on many biological levels (Blair 2004). Most notably, increased urbanization contributes to losses of biodiversity and altered assemblages of species within communities (Blair 1996, Marzluff 2001, McKinney 2002 & 2006, Fischer et al. 2012). Changes in community composition may be explained by variation in tolerance levels of individual species as they encounter transformations in habitat structure, variation in resource availability, and disturbance factors such as increased light, noise, and human activity (Blair 2004, Marzluff 2001, McKinney 2002 & 2006, Marzluff et al. 2015). These changes in community structure often result in the removal or replacement of top predators in urban ecosystems, modifying top-down control within the ecosystem and altering trophic interactions. Because predator-prey dynamics play such an integral role in shaping and regulating wildlife communities (Shochat et al. 2006, Stracey 2011), trickle-down effects from the disruption of this trophic interaction have the potential to produce impacts that are far-reaching. In urban systems, some of these impacts may even be unexpected. For example, recent studies have shown a paradox of increased predator abundance but decreased rates of predation as urbanization increases (Blair 2004, Stracey 2011, Fischer et al. 2012, Eötvös 2018).

Several hypotheses have been proposed to explain this disassociation between the abundance of predators and rates of predation in urban areas, including changes in predator species and prey composition (Sorace & Gustin 2009, Fischer et al. 2012), prey hyper-abundance as a result of increased anthropogenic resource subsidies (Marzluff 2001, Fischer et al. 2012), prey switching by predators (Shochat et al. 2006, Rodewald et al. 2011, Stracey 2011, Malone et al. 2017), and specialization of prey to urban areas (Shochat et al. 2006, Stracey 2011, Malone et al. 2017). These hypotheses are not necessarily mutually exclusive and can be observed in combination with one another. For example, prey switching by generalist predators, such as the

Cooper's hawk (*Accipiter cooperii*), has been observed in densely populated cities where they switch from historic prey to a few native and non-native species, such as rock pigeons and other dove species (*Columba sp.*) that have become over-abundant (Stracey 2011, Malone et al. 2017). These alternate prey species are predictably able to thrive in the resource rich environment provided by increased human presence (Marzluff 2001, McKinney 2006, Stracey 2011). Prey switching has therefore been proposed as a contributing factor to the reduction in predation rates on historic prey species of Cooper's hawks in these urban areas (Stracey 2011, Malone et al. 2017).

It remains unclear whether the decoupling of predator-prey relationships is widespread across all urbanized areas and to what extent this impacts urban ecosystems. Therefore, the goal of this study was to investigate predator-prey dynamics within the Great Trinity Forest, with a focus on the raptor community. Raptors are regularly used as indicators of environmental health (Rodriguez-Estrella et al. 1998, Carrete et al. 2009). Because of their position as an easily monitored top predator, typically associated with high biodiversity, declines in some raptor populations likewise have been shown to reflect a decline in biological integrity of the ecosystem they inhabit (Newton 1979, Carrete et al. 2009). Baseline monitoring of raptor activity and community composition, with associated prey relationships along the urban-to-rural gradient in the Great Trinity Forest will assist in determining the current health of this forest ecosystem.

The Great Trinity Forest is located within the fourth largest metroplex in the United States, Dallas-Fort Worth (U.S. Census Bureau, 2010). This forest "island" has a wide range of disturbance factors typically associated with highly urbanized areas: habitat degradation, invasive species, increased noise and light, and increased presence of humans. The existence of these factors suggest that the Great Trinity Forest is a suitable area to evaluate the relationship of predators and their prey. As a floodplain forest, the Great Trinity Forest also makes an ideal location to quantify predator-prey dynamics by studying raptor predation on water snakes. Preliminary reports indicate there is a large and diverse raptor community within the Great Trinity Forest, and several of the raptors regularly feed on snakes and rodents.

Because observations of natural predation events are infrequent, the use of models has been effective in exploring differences in predation rates between natural and urban areas. Past experiments with birds have primarily used real and artificial nests to assess nest predation (Blair 2004, Borgmann & Rodewald 2004, Stracey 2011, Malone et al. 2017); however, research with other vertebrates such as the green anole (*Anolis carolinensis*; McMillan & Irschick 2010) and Texas horned lizard (*Phrynosoma cornutum*; Mirkin 2019), have used models of the organisms themselves. The use of multiple types of foam prey mimics is a technique, to our knowledge, not yet used to assess predator-prey dynamics along an urban gradient. The purpose of this study is, therefore, to characterize the raptor community and rates of predation on both water snake mimics and an alternative prey source, mice, along the urban-rural gradient in the Great Trinity Forest. We predicted that urbanization would impact raptor predation rates by causing changes in the predator community (e.g., raptor species sensitive to disturbance may disappear from the highly urbanized area) and/or by changing the abundance and availability of prey.

Given that the specific outcomes of altered predator-prey dynamics can be hard to predict, there are least two plausible outcomes from this study. First, it is expected that as urbanization increases, predation rates will decrease, while overall raptor abundance will remain unaffected. This could be due to the exponential increase of prey populations in relation to raptor abundance (Marzluff 2001, Fischer et al. 2012), reductions in specialist and increases in generalist predators (Sorace & Gustin 2008), or transitions in prey composition to species that have become specialized in both exploiting urban areas and avoiding raptors within it (Fischer et al. 2012). These factors would therefore result in an increase of prey survival as top-down control from raptors, dominant predators within the ecosystem, is reduced. This is otherwise known as the predation relaxation hypothesis (Shochat et al. 2006, Stracey 2011, Fischer et al. 2012).

Second, it is plausible to expect that as urbanization increases, raptor abundance will increase, while predation rates will likewise increase. This could be due to increases of generalist raptors as a direct result of perpetually abundant prey items within urban areas that both attract raptors and provide a resource rich environment for optimum reproductive success (Boggie & Mannan 2014). In addition, with the removal of apex predators in more highly urbanized areas, an increase in abundance of mesopredators could contribute to this increase in predation pressure (Rodewald et al. 2011). In this scenario, prey survival decreases as top-down control from raptors increases. This is known as the predator proliferation hypothesis (Fischer et al. 2012). The contradiction between these two possible outcomes (predation relaxation and predator proliferation hypotheses) is known as the urban predation paradox (Fischer et al. 2012).

As human populations grow and urbanization continues to expand into natural areas, it is imperative that biologists are able to predict and manage raptor responses to increased types of disturbance. Since the Great Trinity Forest is located within a large, growing metropolitan area, it is plausible to assume that this encroachment is currently affecting raptor populations and predator-prey dynamics within it. To assess predator-prey dynamics in this urban forest, we identified 4 study objectives: 1) quantify the extent of urbanization with the forest; 2) characterize the composition of the raptor community and quantify raptor activity along an urban-to-rural gradient; 3) quantify predation attempts using prey mimics along the gradient; and then 4) assess the relationship between raptor activity and predation. The results from this study will increase our understanding of raptor predator-prey dynamics along an urban-to-rural gradient and provide insight into how these may be impacted by varying levels of urbanization and disturbance factors associated. This information can then be used to mitigate any associated negative consequences to populations.

METHODS

Study Area

The Great Trinity Forest is a 6,000-acre bottomland hardwood forest located entirely within southeast Dallas, TX in the Blackland Prairie ecoregion (Fig. 1). This forest "island" consists mainly of Eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), cedar elm (*Ulmus crassifolia*), American elm (*Ulmus americana*), hackberry (*Celtis laevigata*), black willow (*Salix nigra*), and pecan (*Carya illinoinensis*) in the overstory. Understory is mainly composed of dogwood (*Cornus florida*), mulberry (*Morus spp.)*, Eastern swamp privet (*Forestiera acuminate*), and the invasive Chinese privet (*Ligustrum sinense*). The Trinity River winds its way southeast through the forest and plays a critical role in ecosystem functions for both year-round and seasonal species.

Light and heavy industry are primarily found on the north and west sides of the forest, intermixed with both impoverished and gentrifying neighborhoods. Municipal utilities for water treatment are located both proximal to downtown Dallas and at the furthest city boundary along the Trinity River to the southeast. A large landfill, multiple golf courses, city parks, a paved trail system, and the Trinity River Audubon Center are also found within and adjacent to the forest. At its farthest reaches to the southeast, agricultural land becomes increasingly dominant. State, U.S., and interstate highways intersect the forest in multiple locations (Fig. 1).

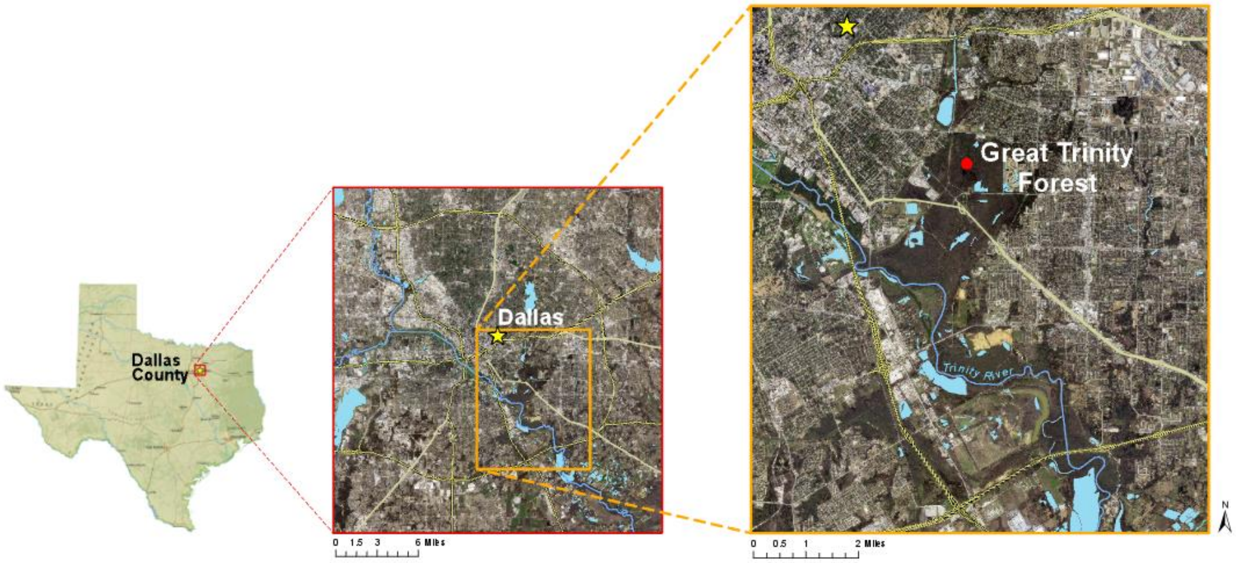

Figure 1. The Great Trinity Forest in Dallas, Texas.

Land Cover Classification and Survey Sites

To classify land cover within the forest, we obtained a 2016 50-cm pixel resolution, multi-band remote sensing image of the forest and surrounding Dallas County from the Texas Natural Resource Information System (tnris.org). Using ArcGIS Pro’s (version 2.2.0) image classification wizard with supervised, object-based classification, we processed and reclassified the forest into four land cover categories: impervious surface, forest, open water, and grass/cultivated land (Fig. 2). We defined impervious surfaces as any man-made material that is impenetrable to water (e.g., roofs, concrete, building materials, etc.).

Using the above land cover information as well as first-hand knowledge of habitat types within the forest, locations of trails and pathways, and forest access points from within the surrounding matrix, we identified 3 suitable survey locations within the Great Trinity Forest (Fig. 2). At each survey location (hereafter “site”), we established 6 raptor survey stations spaced approximately 650 m apart along a transect that could be accessed on foot or by bicycle (see next section). The locations of these 3 sites followed the urban-to-rural gradient, extending from downtown Dallas in the northwest toward the southeast, and as such, were characterized by differing levels of urbanization. For our purposes, we defined urbanization as the percentage of impervious surface present within the forest and the nearby matrix. Since the final classification of land cover was a raster-based map with pixels as its base unit, we determined the percent of impervious surface within a 5 km^2 buffer of each raptor survey station by dividing pixels classified as “impervious” within each buffer by the total number of pixels and then multiplied by 100. We then repeated this process for the remaining 3 landcover categories for each raptor survey location. The 5 km^2 area analyzed per raptor survey station was selected because it encompassed the extent of the breeding territories of raptor species known to inhabit the forest (Billerman et al. 2020; T. K. Stevens, personal comm.). Using this method, we categorized our 3 sites as “low” urbanization (14-16% impervious surface), “medium” urbanization (18-23%), and “high” urbanization (27-43%).

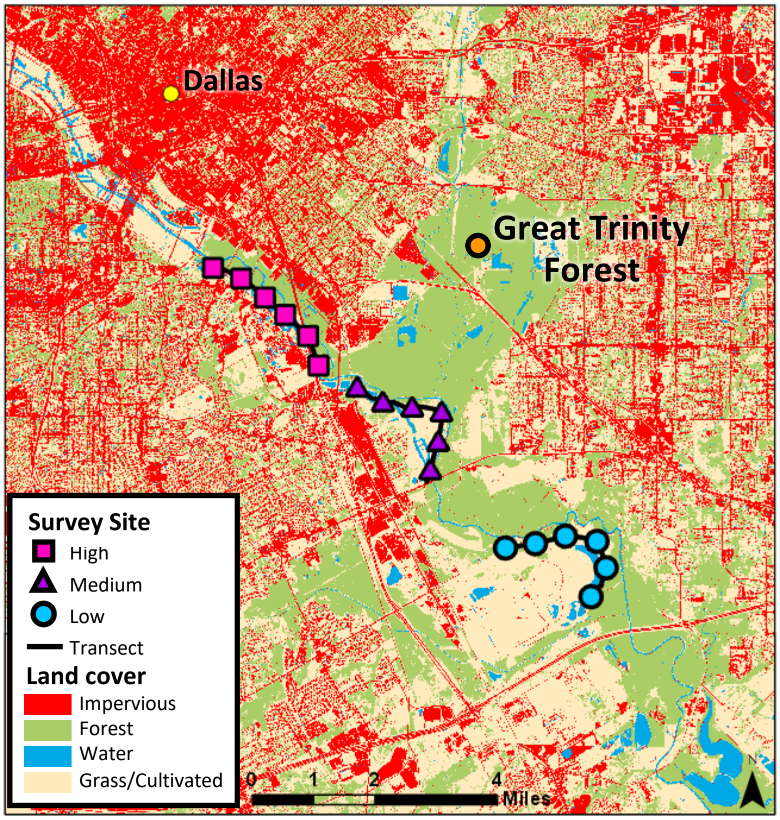

Figure 2. Study area within the Great Trinity Forest in Dallas, TX. Three study sites with differing levels of urbanization were assessed for raptor activity/use and rate of predation: high (pink squares), medium (purple triangles) and low (blue circles). Individual shapes indicate raptor survey stations along transects. Land cover was assessed using ArcGIS Pro (version 2.2).

Raptor Activity

We assessed raptor activity at 6 survey stations within each site (Fig. 2; n = 18 survey stations) along the urban-to-rural gradient using conspecific broadcast call surveys following protocols established by Fuller and Mosher (1981, 1987, 1996), Mosher et al. (1990), and Rullman and Marzluff (2014). The survey stations were approximately 650 m apart to avoid overlap of species counts due to raptor mobility and the audible range of their calls. Our survey methods were consistent with published guidelines for the use of playbacks with wild birds in research (Fair et al. 2010). Species calls were downloaded from xeno-canto (xeno-canto.org) and uploaded onto a FoxPro Fusion wildlife caller. Every attempt was made to use raptor calls that were recorded as close to the study area as possible. The order in which the species calls were initially played was determined by species size and then aggressiveness (i.e., from smallest to biggest and least to most) to avoid incidental predation of smaller species by those that were larger or more aggressive. The resulting species broadcast order was: 1) Cooper's hawk (*Accipiter cooperii*), 2) red-shouldered hawk (*Buteo lineatus*), 3) red-tailed hawk (*Buteo jamaicensis*), 4) barred owl (*Strix varia*), and 5) great-horned owl (*Bubo virginianus*). Great-horned owl calls were additionally broadcasted last due to the ability of calls to elicit territorial responses from other raptor species if conspecific calls themselves were not successful (Fuller and Mosher 1987 & 1996, Rullman and Marzluff 2014).

During surveys, we mounted the FoxPro caller to a tripod raised to 2 meters above ground level. The initial broadcast duration for an individual species was 1 min followed by 2 minutes of silence to observe responses. We then re-positioned the caller 90° and repeated the broadcast for 1 min followed by another 2 min of silence. Since the FoxPro Fusion caller was equipped with 2 speakers facing opposite directions, this approach provided 360° of broadcast coverage for a total of 6 minutes of survey time for each species at each station. During these surveys, we recorded all aural and visual observations of raptors including raptor species, bearing, distance, and activity, if possible.

We conducted surveys weekly between sunrise and 1500 from late May to early August 2019. We rotated the order in which we surveyed the 3 sites, as well as the 6 stations within sites, on a weekly basis to minimize the confounding factors associated with time of day. In all subsequent analyses we removed the observations of American kestrels (*Falco sparverius*) as this species was only observed at one station, and compared to the other raptors in the Great Trinity Forest, it is the least likely to consume snakes as its diet is comprised mainly of insects (Balgooyen 1976, Yáñez et al. 1980). We estimated raptor activity at each station by calculating the average number of raptors observed at each station over the 10-week survey period. Activity within each of the three sites was likewise calculated as the average number of raptors observed per site over the survey period. We also calculated the Shannon Equitability Index ($E_H = H/log(k)$) to estimate raptor diversity at each survey location. This index normalizes the Shannon Diversity Index (H) into a range of values from 0 to 1, with 1 indicating the highest diversity.

Prey Mimic Models

We created models to mimic two main raptor prey types in our study area: snakes and mice. Utilizing mimics as prey items has proven to be a valuable method to detect and estimate predation rates for a range of vertebrate species (Brodie 1993, Farallo & Forstner 2012, Bateman et al. 2017, Mirkin 2019). We used urethane foam to make our models because this material allows for accurate identification of predator species through marks left on the models (e.g., raptor talons, beaks, teeth marks from rodents, etc.; Brodie 1993, Bateman et al. 2017) and can withstand temperatures in excess of 38°C, which is necessary for use north-central Texas environments during the summer months (Farallo and Forstner 2012). SmoothOn Mold-Max 29®, a silicone-based rubber mold kit, was used to create casts for prey models using realistically detailed plastic snakes and mice as prototypes. Models were then made by injecting SmoothOn Flex Foam-it! 3® urethane foam mixed with UV resistant black paint into casts. We made foam snakes of 2 different sizes (small - 8” length x 1” diameter, and medium - 1.5’ length x 2” diameter; Fig. 3a,b), which allowed for preferences or difference in prey size among the different raptor species. We made foam mice (3.5” length (not including tail) x 2.5” diameter in the mid-section) as an alternate prey item for raptors (Fig. 3c). Our control models were the shape of a triangular prism (3” height x 5” base x 4” width), made from a cast of a large Toblerone chocolate bar box (Fig. 3d). UV resistant black paint was mixed with the foam solution to create black snake and grey mice models that were like a variety of native water snakes and mice within the forest. The control models were also black.

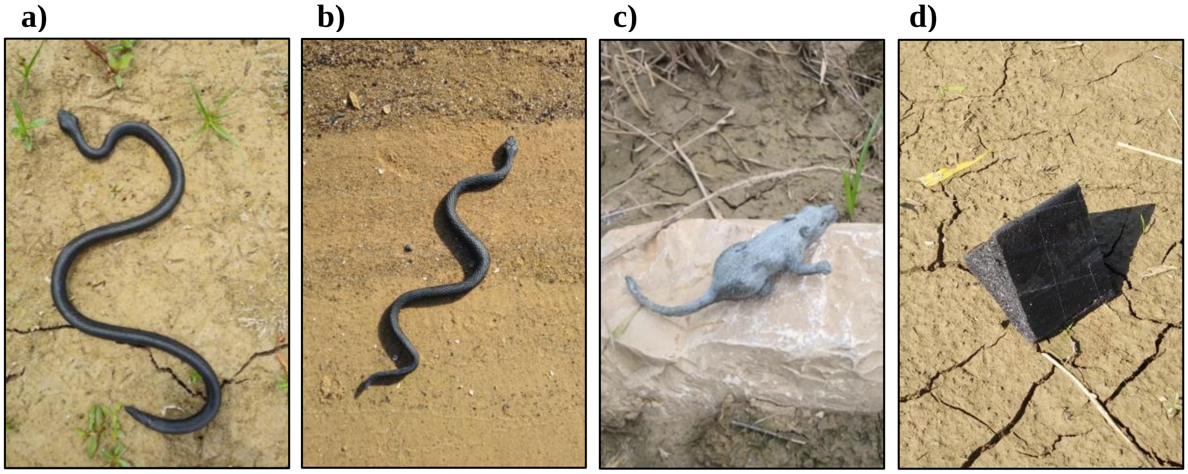

Figure 3. Urethane foam prey models: a) medium snake (1.5’ length x 2” diameter), b) small snake (8” length x 1” diameter), c) mouse (3.5” length (not including tail) x 2.5” diameter in the mid-section), and d) control (3” height x 5” base x 4” width).

From mid-June to early August 2019, we placed prey models and controls within 150 m of each raptor survey station in all 3 sites. Initially, one model of each type (small snake, small snake, mouse, and control) was placed at each station and tethered to a metal stake with 6 lb. fishing line (n = 72 models). We placed models in locations that seemed to be logical places for the prey species type and that were visible to raptor species searching for prey (i.e., on bare ground or in open areas with low vegetation, open canopy, and near water sources) and were consistently accessible. We checked the models every 7 days; those with marks from predators were considered to have had a predation event and were subsequently removed from the study site. Models that were damaged (e.g, discolored by sun or water, crushed by foot or vehicle traffic, covered in dirt, etc.) were also removed. Models in pristine condition were collected and redeployed to a different location at the survey station along with one new model of each type. We repeated this process weekly until the end of the study period, ensuring there was a consistent and uniform abundance of prey mimic types across the urbanization gradient.

We had access to 20 field cameras that we could strategically place near models to capture predation events, characterize the predator community (which also included mammals and wading birds), and aid in the identification of the predator marks to species. These cameras were also checked and rotated among models on a weekly basis. We reviewed the data files from each camera to match predator to prey marks if a predation event had occurred and to otherwise improve camera placement as the study progressed.

To aid in accurate verification of raptor depredations, Window to the Wild, a non-profit organization specializing in raptor education to the public, assisted us by presenting small (n = 20) and medium (n = 20) snake models to red-tailed hawks and great-horned owls at their facility and recording observations of raptor behavior when the models were being attacked. We compared the condition (i.e., number and location of breaks, pressure marks, etc.) of the models that were attacked at this facility to depredated models collected from the Great Trinity Forest. This comparison increased our confidence in categorizing the depredation events in the Great Trinity Forest to the following 5 predator types: raptor, wading bird, feral hog, rodent, and mesocarnivore.

Statistical Methods

For the analysis of raptor activity and impervious surface, we first calculated the proportion of total raptor observations that occurred at each survey station. As transformations failed to correct for non-normality and unequal variance in raptor activity, we used Spearman's rank correlations to examine the relationship between raptor activity and the percentage of impervious surface. Due to the high variation in observed raptor activity at the "medium: urbanization sites (see results and discussion), we also treated the percentage of impervious surface as a categorical variable and compared raptor activity between the "high" and "low" sites (n = 6 survey locations each) using ANOVA.

We used Fisher's Exact tests to compare the proportion of attacks on the different prey mimic types and to the control models. For the analysis of predation attempts and impervious surface, we present the frequency of predation attempts on models as the proportion of total depredations for each model type for each survey station to control for differences in the total number of deployed models of each type across sites and stations. We used Pearson's correlations to example the relationship between the proportion of predation attempts and the percentage of impervious surfaces for the various model types. We conducted each of the analyses the following two ways: 1) counting missing models as "depredations" and 2) removing missing models entirely from the analysis. As we found no significant differences in patterns between these two types of analyses, we only present results with the missing models removed.

As raptor predation attempts were only observed on the snake models (see results), we used linear regression to analyze the relationship between the proportion of raptors present and the proportion of predation attempts on snakes along the urbanization gradient (n = 18 survey locations). Like the approach we used for raptor activity, we also treated the percentage of impervious surface as a categorical variable (using extremes only) and compared the proportion of predation attempts on snakes between the "high" and "low" sites using a Fisher's exact test. For all analyses, $\alpha = 0.05$.

RESULTS

Land Cover Classification Along the Urbanization Gradient

The extent of impervious surface varied among the urbanization sites, increasing from the low to high site, ranging from 14.1% to 42.6%, respectively (Table 1). Grass/cultivated land cover revealed an inverted pattern, increasing from the high to low urbanization site, ranging from 32.4% to 50.3%, respectively. The percent of open water remained consistent between the 3 sites, with very little variation, ranging from 2.8% to 3.8%. The greatest variation of this land cover type was found in the low urbanization site, which contained both extremes of the percentage range (mean = 3.2 ± 0.3 SD, n = 6). Forest cover across the 3 sites ranged from 21.9% to 38.5%, peaking in the medium urbanization site (mean = 37.7 ± 0.6 SD, n = 6). We predictably found the lowest percentage of forest cover within the high urbanization site (21.9%, mean = 27.7 ± 4.4 SD, n = 6).

Raptor Activity

In total, we observed 161 raptors representing 8 species within the study area during the 10-week survey period. In addition to the 5 species represented in the call playbacks, we observed Swainson's hawks (*Buteo swainsoni*), Mississippi kites (*Ictinia mississippiensis*), and American kestrels. We found the overall greatest number of raptors within the low urbanization site with a total of 75 raptors detected. The high and medium sites followed with 48 and 38 raptors, respectively. We observed this trend throughout the study period with the low urbanization site containing the highest weekly average activity with few exceptions (Fig. 4).

Table 1. The percentages of impervious surface, forest, open water, and grass/cultivated land within a 5 km^2 buffer at 6 raptor survey locations at 3 survey sites within the Great Trinity Forest, Dallas, TX.

		Study Site		
		High Urbanization	**Medium Urbanization**	**Low Urbanization**
Impervious surface	Range	26.8 - 42.6	17.7 - 23.1	14.1 - 15.5
	Mean ± SD	34.6 ± 6.1	19.9 ± 1.9	15.1 ± 0.6
Forest	Range	21.9 - 33.3	36.9 - 38.5	31.8 - 35.4
	Mean ± SD	27.7 ± 4.4	37.7 ± 0.6	33.6 ± 1.5
Open water	Range	3.0 - 3.3	3.1 - 3.5	2.8 - 3.8
	Mean ± SD	3.2 ± 0.1	3.3 ± 0.2	3.2 ± 0.3
Grass/cultivated	Range	32.4 - 36.7	36.7 - 42.0	46.5 - 50.3
	Mean ± SD	34.5 ± 1.7	39.2 ± 2.0	48.1 ± 1.7

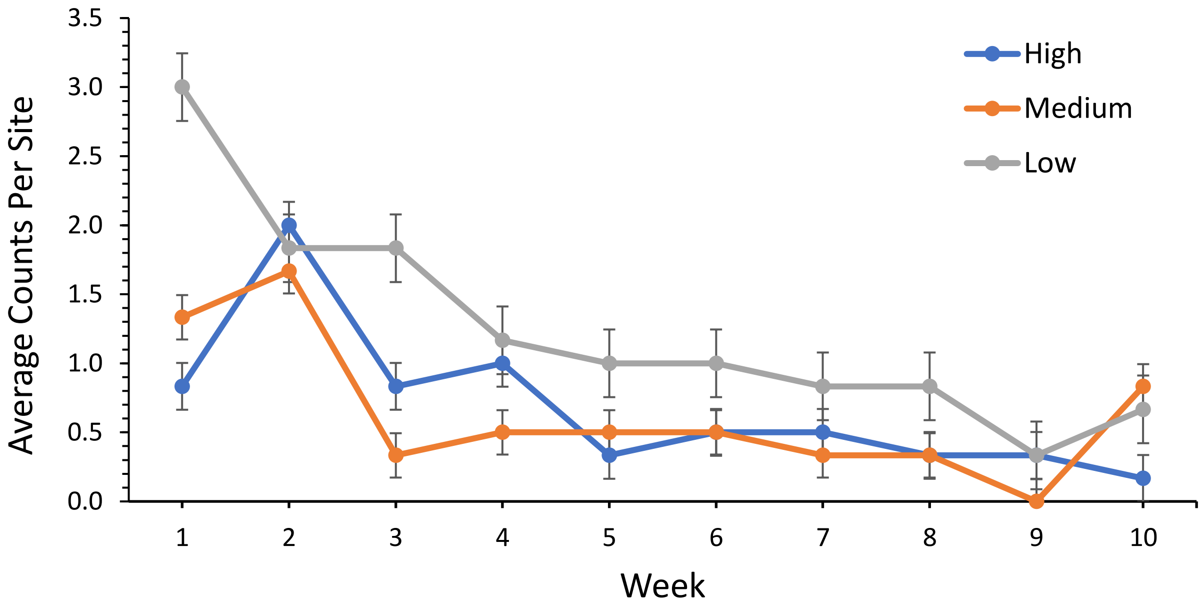

Figure 4. Average raptor counts (±1 SE) in each urbanization level in the Great Trinity Forest, Dallas, TX over the 10-week study period.

Our comparison of average raptor activity along the gradient revealed variation across the entire study area (Fig. 5). Red-tailed hawks, red-shouldered hawks, and Mississippi kites were relatively ubiquitous throughout (Fig. 6). In general, red-shouldered hawks were the most active species across the gradient and, along with the Mississippi kite, were observed to be more active in medium to low urbanization stations. Red-tailed hawks, on the other hand, were overall more active at stations with high to medium-high urbanization. A few raptor species were only observed at a small number of survey locations. We only observed barred owls, for example, within areas of low urbanization.

We found no significant relationship between raptor activity and level of urbanization (i.e., percent impervious surface; $r_s = -0.443$, $p = 0.066$, $n = 18$ stations; Fig. 7). Raptor diversity, as measured by the Shannon Equitability Index, ranged from 0.86 at the highest level of urbanization to 0.91 at the lowest level of urbanization (mean = 0.76, SD = 0.29, n = 18 stations). When we treated urbanization as a categorical variable (high and low), however, the mean proportion of raptor activity was significantly higher in the low urbanization site compared to the high urbanization site (One-way ANOVA: $F_{1,10} = 14.95$, $p = 0.003$: Fig. 8).

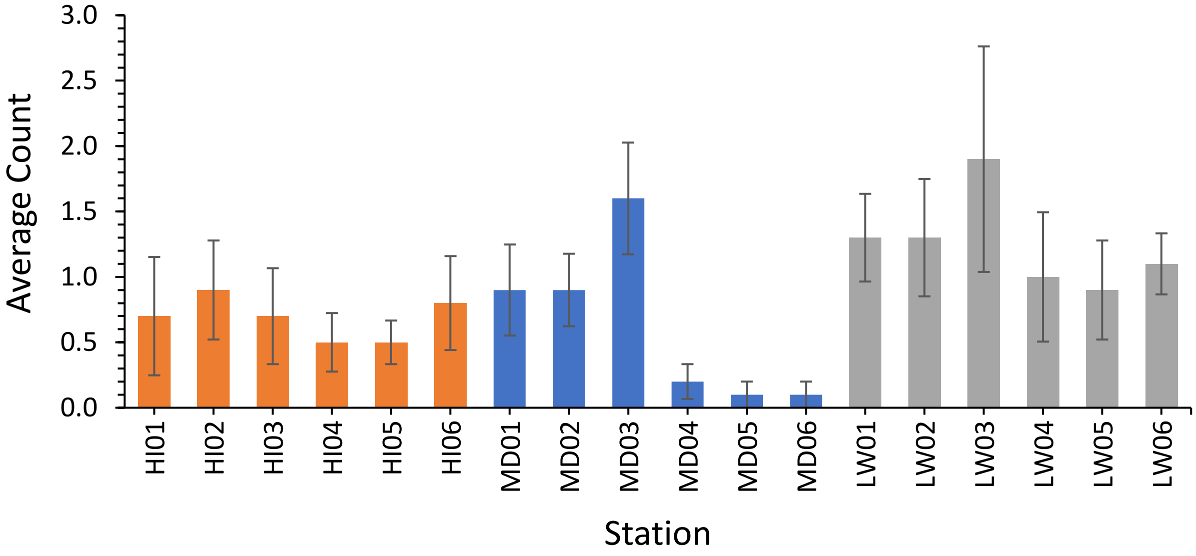

Figure 5. Average raptor counts (±1 SE) per raptor survey station over a 10-week survey period in the Great Trinity Forest, Dallas, TX.

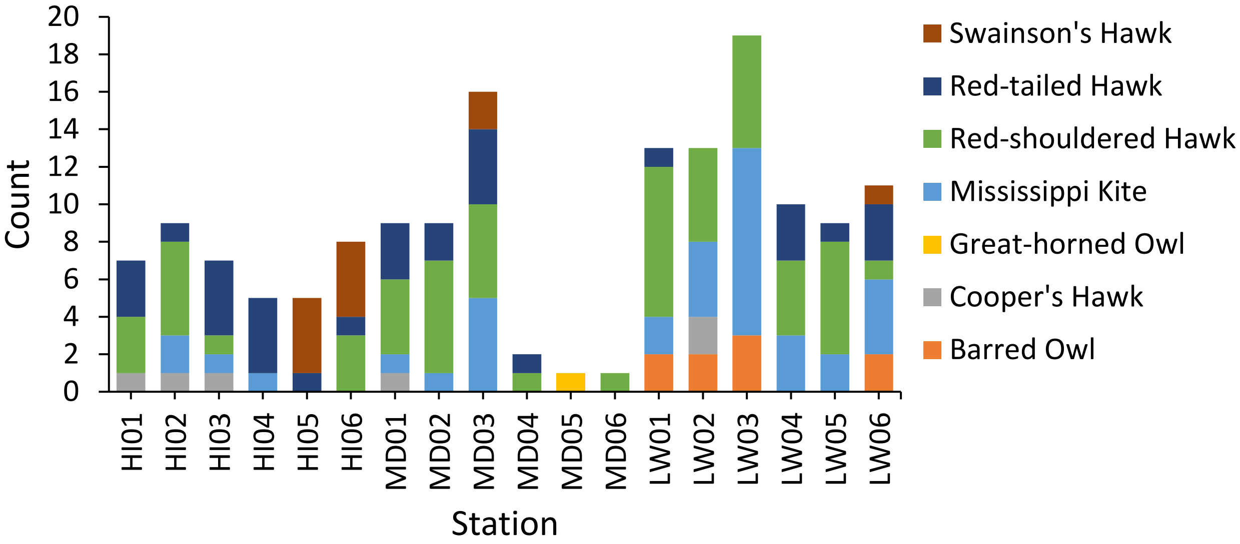

Figure 6. Species richness within each raptor survey station along the urban-to-rural gradient in the Great Trinity Forest, Dallas, TX. "HI01" indicates the station with greatest level of urbanization while "LW06" indicates the station with the lowest level of urbanization. American kestrels are not shown.

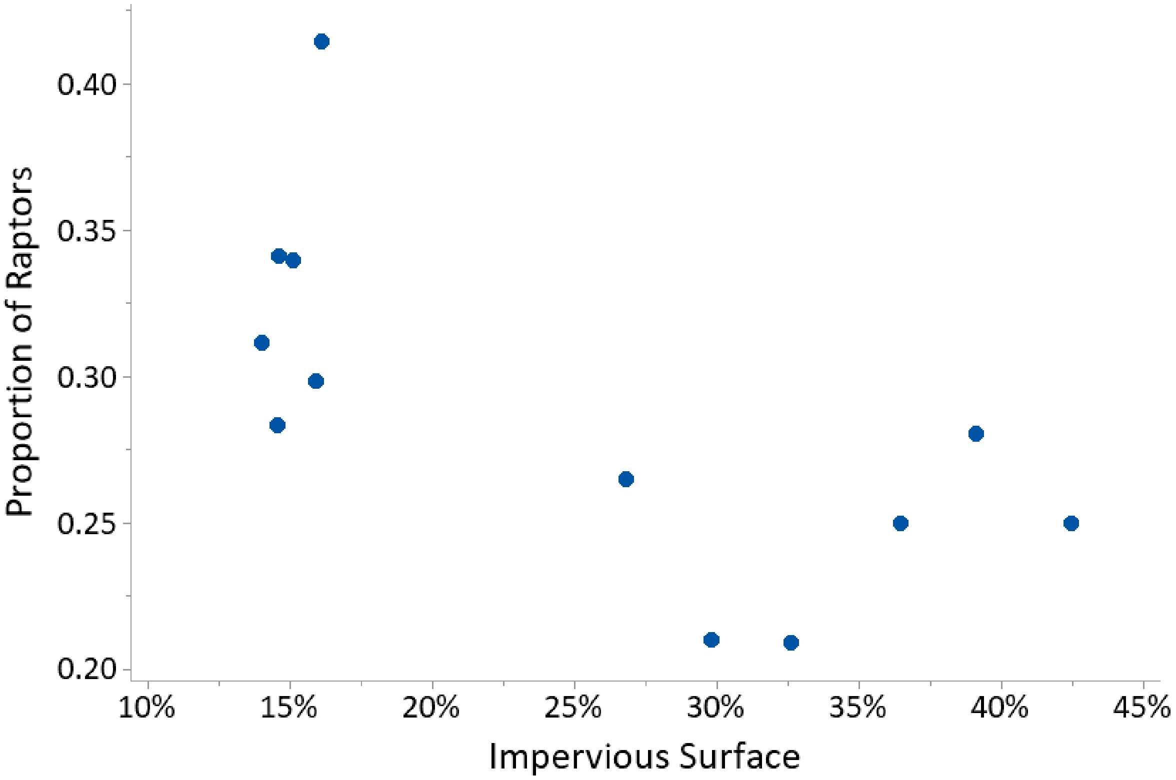

Figure 7. No correlation between proportion of total raptors observed and percent impervious surface along the urban to rural gradient in the Great Trinity Forest, Dallas, TX during the 10-week study period (n = 18, Spearman's rank correlation, p = 0.066). Proportion of raptors was transformed using an arcsine square root transformation.

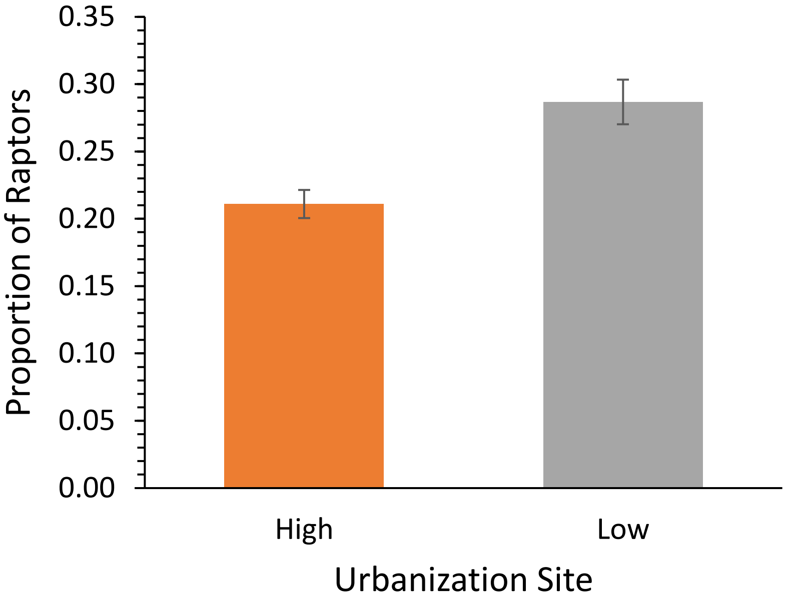

Figure 8. Average total proportion of raptors (±1 SE) in high (n = 6) and low (n = 6) areas of urbanization in the Great Trinity Forest, Dallas, TX over the 10-week study period. Data was transformed using an arcsine square root transformation.

Predation Attempts on Prey Mimics

We deployed a total of 732 urethane foam prey models throughout the study period (Table 2). Sixty-one models were confirmed depredated and 23 models were missing when checked and never recovered. It is feasible to assume that these missing models were depredated; however, as this cannot be verified, we have omitted the missing models from further analysis and discussion. The proportion of predation attempts was significantly higher for small and medium snake models compared to controls (Fisher's exact test: medium snake vs. control, p = 0.004; small snake vs. control, p = 0.026). In contrast, the proportion of predation attempts on mouse models did not differ from the controls (Fisher's exact test: p = 0.223). When comparing the prey mimic types to each other, we found no significant difference in the proportion of predation attempts (Fisher's exact test: medium snake vs. small snake, p = 0.518; small snake vs. mouse, p = 0.449; medium snake vs. mouse, p = 0.152). Therefore, we decided to combine medium and small snakes together, but left mice separate for all subsequent analyses.

Table 2. Distributions of urethane foam models, per type, with associated depredation and missing counts, within each study site in the Great Trinity Forest, Dallas, TX.

	STUDY SITE					
PREY TYPE	**HIGH**	**MEDIUM**	**LOW**	**TOTAL**	**DEPREDATIONS**	**MISSING**
Medium Snake	70	66	59	195	24	3
Small Snake	63	72	68	203	19	12
Mouse	53	56	44	153	11	6
Control	68	60	53	181	7	2
TOTAL	254	254	224	732	61	23

Using a combination of markings and breaks to the models, camera footage, and observations from Window to the Wild, we assigned a predator type (raptor, wading bird, feral hog, rodent, or mesocarnivore) to each of the 61 depredated models (Fig. 9). Raptors attacked 4.5% of all deployed models and were responsible for 52.5% of all depredation events, greater than any other predator type we identified. Raptors exclusively depredated snake models and were overall the primary predator of this prey type. Because of the force with which raptors hit snake models, depredations were primarily characterized by broken models, typically into 3 or more pieces (Fig. 10a). Pressure marks left by talons were usually absent, but occasionally observed. Beak marks left on the dorsal side were common, ranging from deep indentations to shallow scrapes, generally midline or close to the head. The heads of models were occasionally missing. The only raptor caught on a field camera was one juvenile red-shouldered hawk that approached but did not attack the associated model.

Although mesocarnivore and wading bird depredations also often resulted in broken snake models, these predators also left diagnostic marks (Fig. 10b). Mesocarnivore attacks were characterized by the presence of small, triangular teeth marks at and around breaks or full and partial bite marks without breaks, accounting for approximately 2% of all models deployed and

23% of all depredation events. In contrast, wading bird attacks were primarily characterized by stab marks to the head, but also exhibited talon marks on the ventral side, close to breaks (Fig. 10c). Wading birds only attacked medium snake models. Rodent and feral hog depredations were likewise primarily characterized by teeth marks on prey models (Fig. 10d,e). Many rodent depredations were found with small chewed areas on distal ends of models. A few medium snake models exhibited multiple rows of chew marks with even spacing.

The overall depredation rate on the snake models was 11.2%, with no significant relationship between the proportion of snakes depredated and level of urbanization at the survey sites (Pearson's correlation: r = 0.029, p = 0.911, n = 18; Fig. 11). The overall depredation rate on mouse models was 7.5%, and we did find a significant negative relationship between the proportion of predation attempts and the level of urbanization at the survey sites (Pearson's correlation: r = -0.491, p = 0.0380, n = 18; Fig. 11). And as expected, we found no relationship between predation attempts on the control models (overall depredation rate was 3.9%) and the level of urbanization (Pearson's correlation: r = 0.025, p = 0.922, n = 18; Fig. 11).

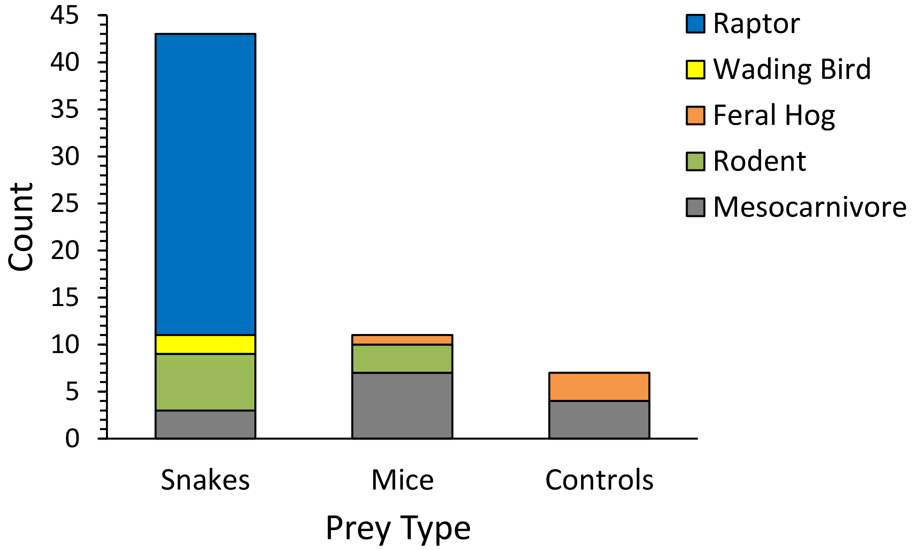

Figure 9. Total depredations of snake (n = 43 of 398) and mouse (n = 11 of 153) prey mimics, as well as controls (n = 7 of 181) by predator type (raptor, wading bird, feral hog, rodent, and mesocarnivore). Predator type was determined by marks left on prey mimics and/or field camera identification.

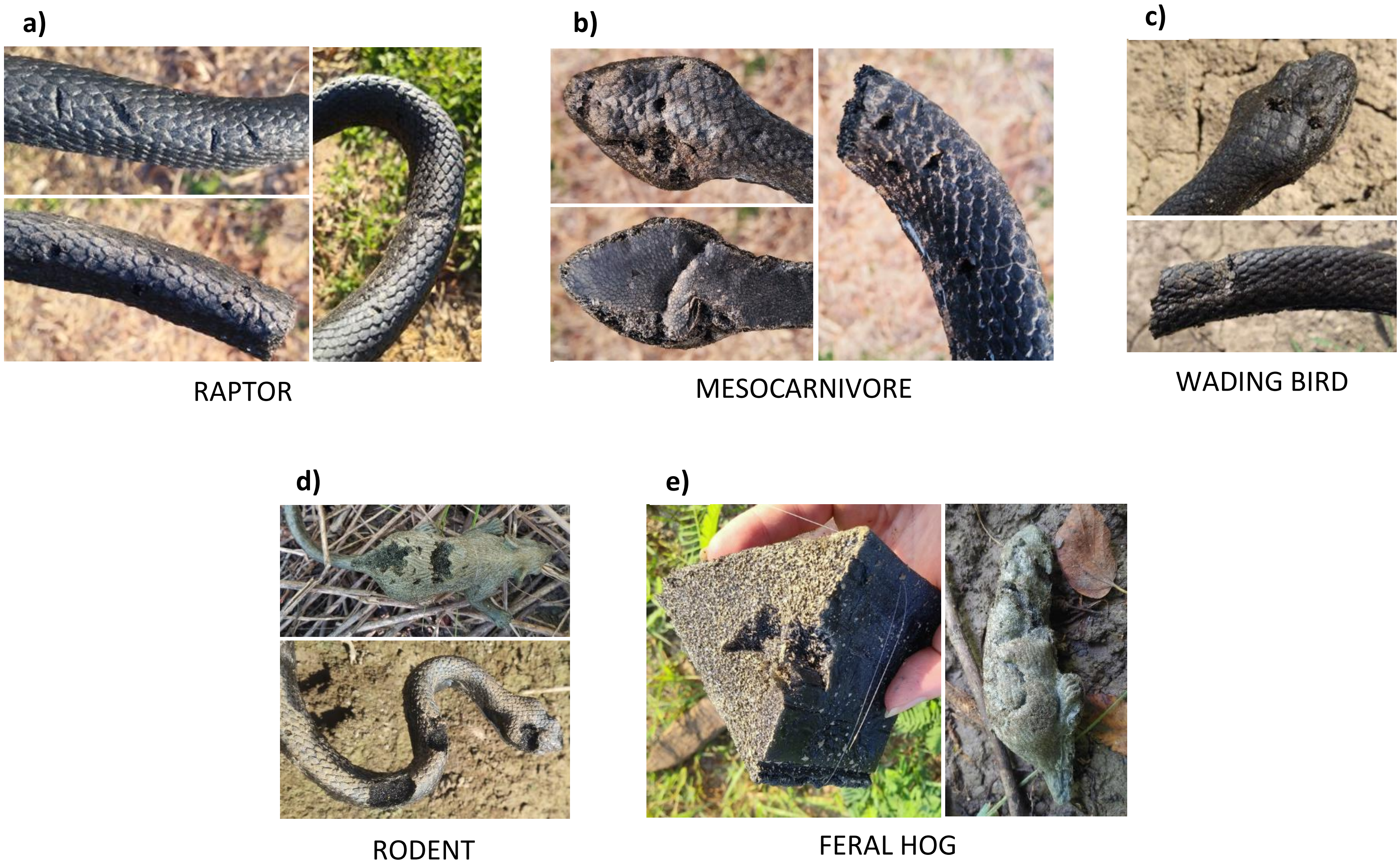

Figure 10. Characteristic depredation marks left by each predator type. These marks were used for accurate identification of predator per depredated model. a) Raptor beak (left) and talon marks (right), b) Mesocarnivore full bite (left) and teeth marks (right), c) Wading bird beak (top) and talon marks (bottom), d) Rodent gnaw (top and bottom) and teeth marks (top), and e) Feral hog teeth marks.

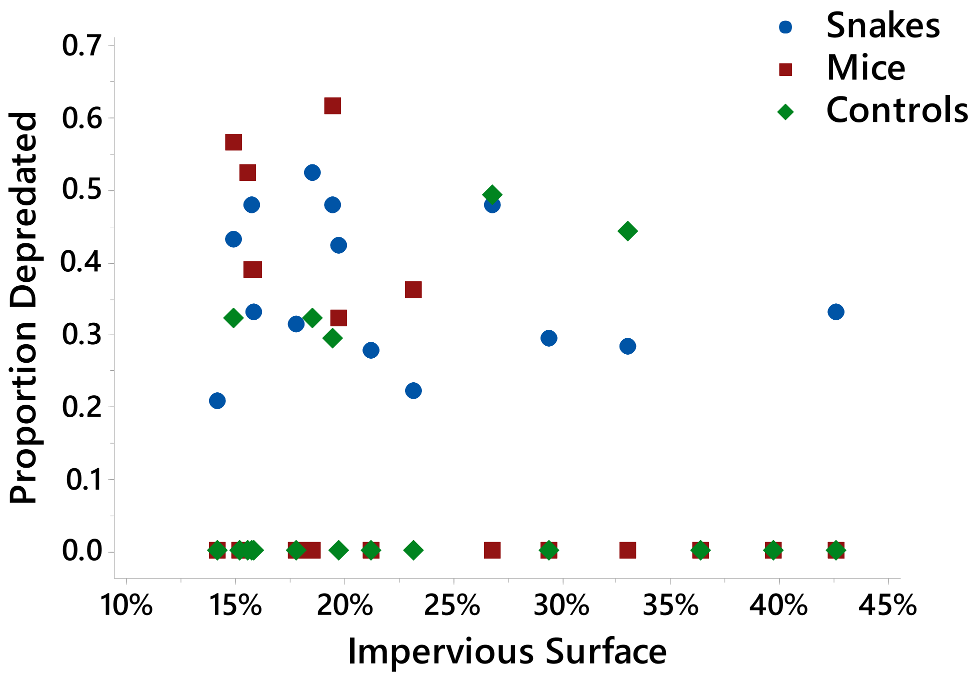

Figure 11. No correlation between percent impervious surface and the proportion of models depredated, per model type, along the urban to rural gradient (n = 18, Pearson's correlation, snakes, p = 0.911; mice, p = 0.038; controls, p = 0.922). Proportion of prey mimic depredations was transformed using an arcsine square root transformation.

When we treated urbanization as a categorical variable (high vs. low), we found no significant difference in the proportion of depredations on snake models between the high and low urbanization sites but significantly less depredations on mice models within the high urbanization site (Fisher's Exact test: snakes - p = 0.674, mice – p = 0.007).

Raptor-Prey Dynamics

Because raptors appeared to target the snake mimics with no evidence of predation attempts on mice, we restricted our analysis of raptor-prey dynamics to snake models only. Across the urbanization gradient, we found no significant relationship between raptor snake depredations and level of urbanization (Pearson's correlation: r = 0.072, p = 0.778; Fig. 12). When we treated urbanization as a categorical variable (high vs. low) and looked at just raptor predation on snakes, we found no significant difference between the 2 study sites (Fisher's Exact test: p = 0.440). Likewise, we found no significant relationship between the proportion of snakes depredated by raptors and proportion of raptors observed at any point along the urban to rural gradient, thus showing a clear disassociation between the abundance of raptors and predation attempts on prey mimics (Fig. 13).

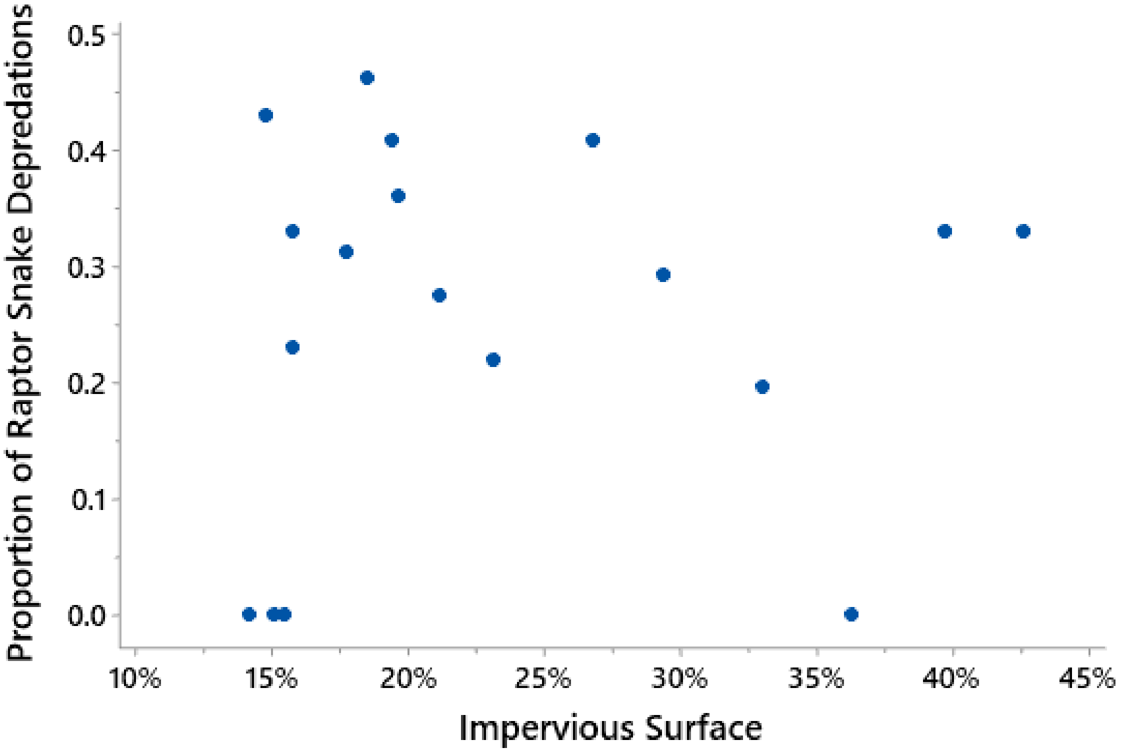

Figure 12. No relationship between proportion of raptor snake depredations and percent impervious surface along the urban to rural gradient in the Great Trinity Forest, Dallas, TX (n = 18, Pearson's correlation, p = 0.778). Proportion of raptor snake depredations was transformed using an arcsine square root transformation.

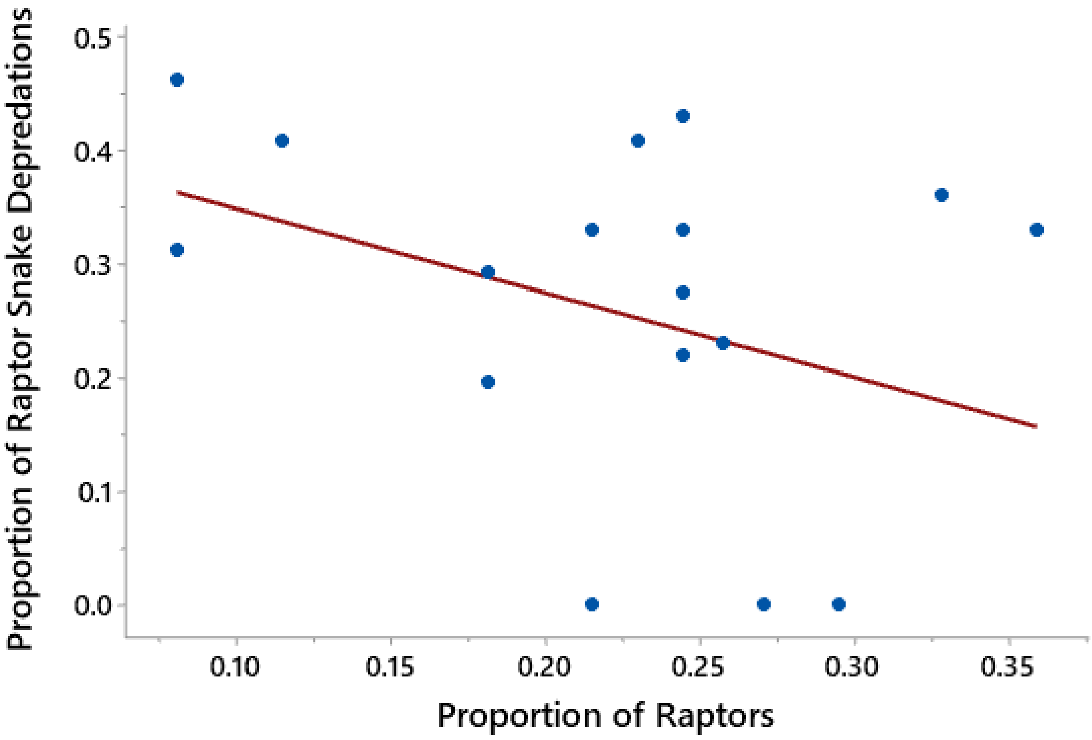

Figure 13. No relationship between the proportion of total snakes depredated by raptors as a function of the associated proportion of total raptors present along the urban to rural gradient in the Great Trinity Forest, Dallas, TX. The line represents the best fit line to the data (n = 18, linear regression, $y = -0.739x + 0.423$, $R^2 = 0.131$, $p = 0.140$). Proportion of raptor snake depredations and proportion of raptors were transformed using an arcsine square root transformation.

DISCUSSION

Urbanization is influencing land-use changes across the globe at an unprecedented rate (Shochat et al. 2010). The conversion of historically natural habitat to developed areas has been shown to alter the composition of wildlife communities within ecosystems as species sensitive to urbanization are replaced by those able to exploit this new environment (McKinney 2006). These changes have been shown to disrupt a critical dynamic of ecosystem function, predator-prey dynamics, with the loss and change in community composition of both predator and prey species.

This study was conducted to determine what degree, if any, increased urbanization impacts the relationship between raptors and their prey within the Great Trinity Forest. As top predators, the health of raptor communities is typically a useful indicator of overall ecosystem fitness by observing changes in species populations and fitness (Newton 1979, Lambeck 1997, Rodriguez-Estrella et al. 1998, Carrete et al. 2009). This is especially evident in urban areas, as raptors can be sensitive to human disturbance and environmental degradation (Newton 1979). However, some generalist raptor species (in regard to diet and/or habitat use) have been increasingly found to adapt and colonize areas along urban gradients, even with these factors present.

We discovered no relationship between raptor activity or diversity and degree of urbanization along the entire urban-to-rural gradient within the Great Trinity Forest. However, when only the extremes of the gradient were evaluated (i.e., the “high” and “low” sites), we found raptor activity to be significantly less in the area with higher levels of urbanization. Regardless of our method of assessment, both the overall proportion of snake model depredations and proportion of raptor snake depredations did not vary significantly with changes in urbanization.

Mice mimics showed a significant decrease in predation attempts as urbanization increased. In fact, we discovered zero attacks on mice within the entire high urbanization site throughout the study period. It is possible this reduction in predation is due to increased abundance of other rodents or prey items as urbanization increased, making it less likely these mimics would be targeted. Mesocarnivores were found to be the primary predator type attacking mice mimics in our study system. If mice or other small rodents were the preferred prey items of particular mesocarnivore species that avoided higher levels of urbanization, then this could also explain this reduction in predation. Alternatively, many mesocarnivores are considered generalists and typically would not be sensitive to increases in urbanization, suggesting that the predation relaxation hypothesis is a more likely explanation for this result.

Central to our overall study goal, we found no significant relationship between raptor activity and raptor predation on snake models within the Great Trinity Forest. This lack of relationship points to an unexplained disassociation in raptor-prey dynamics and requires further examination. These results suggest that either increasing levels of urbanization have no effect on raptors-prey dynamics within the Great Trinity Forest or that there is low predatory response from raptors to the prey mimics. Alternatively, it is possible we were unable to detect the predation-paradox due to the limited extent of our urbanization gradient, limited quantity of data that could be collected within a single field season, or other factors not yet assessed within the forest. Future studies should extend the urban-to-rural gradient so that more extreme levels of urbanization may be captured. As an alternative, a comparative study could be conducted to measure differences in predator-prey dynamics between the Great Trinity Forest as a whole and a separate, similar study area with no urbanization.

Of the 8 species of raptors detected, all can be described as generalists (Kalla & Alsop 1983, Bird & Palmer 1988, Rosenfield & Bielefeldt 1993, Marti & Kochert 1996, Mazur & James 2000, Preston & Bean 2009, Bechard et al. 2010, Strobel & Boal 2010). Similar to this study, other studies have found no significant change in the frequency of generalist avian species when urbanization increased along a gradient (Sorace & Gustin 2009). It has been shown that when a raptor community contains many generalist species, their presence can lose its ability to reflect habitat degradation (Rodriguez-Estrella et al. 1998, Swihart et al. 2003). Given the large home ranges and niche breadths of these raptor species, combined with the absence of any extremes in urbanization along the gradient, it is possible the raptors within the Great Trinity Forest are using the forest as a whole to hunt, rather than specific areas with particular levels of urbanization (Swihart et al. 2003). If this were the case, it would be difficult to detect any effects of urbanization on raptor-prey dynamics.

Nonetheless, when we analyzed only extremes of the gradient ("high" and "low" sites), raptor activity was significantly lower in areas of high urbanization. The "medium" study site had urbanization levels that were similar to the "low" site, but raptor activity was much more variable with half the survey locations having zero raptor observations. We are uncertain as to why we observed so few raptors at these survey stations as the distribution of land cover types, proximity to water, etc. was not strikingly different. We did notice, however, that these sites had high levels of ragweed (*Ambrosia trifida*) that grew as a monoculture in disturbed areas that likely impeded the ability of raptors to effectively hunt at those locations. Our omission of the potentially uncertain data from the "medium" sites may have revealed the true effects of urbanization on raptor activity in high urban areas of the Great Trinity Forest. The absence of more specialized raptor species, such as bald eagles (*Haliaeetus leucocephalus*) and osprey (*Pandion haliaetus*), throughout the gradient may by itself point to negative changes in the raptor community as a result of factors associated with urbanization.

Overall depredation rate of snake models (11.2% excluding missing models) and depredation rate of raptors (6.0%) were similar or lower than other studies involving prey mimics, aside from non-stationary models in Paluh et al. (2014) (Saporito et al. 2007 (12.4% overall, 8.9% avian), Valkonen et al. 2011 (26.7% overall, 8.2% raptors), Farallo & Forstner 2012 (13% overall, 6% avian), Paluh et al. 2014 (stationary models: 13% overall, 4% avian; non-stationary: 18% overall, 9% avian)). Removing "medium" areas of urbanization produced similar depredation rates (9.0% total, 5.0% raptors). Many studies used a similar number of deployed models, but most measured discrete variables such as responses from predators based on difference in color, pattern, head shape, or movement from models (Brodie 1993, Saporito et al. 2007, Valkonen et al. 2011, Farallo & Forstner 2012, Paluh et al. 2014, Bateman et al. 2017). Differences in predator response may be more difficult to ascertain along a gradient using continuous variables when there are such low rates of predation overall. In this case, it would be difficult to determine patterns with just one study. With additional data we could increase our confidence in the true effects of urbanization on raptor-prey dynamics.

Additionally, models deployed within the forest were stationary. Raptors are visual hunters (Farallo & Forstner 2012) and may be less able to detect or even recognize immobile models as prey items (Paluh et al. 2014). Predators are, in general, more likely to attack moving rather than stationary prey (Heinenand & Hammond 1997, Paluh et al. 2014). Intermittent movement incorporated into prey models has been shown to create more realistic prey, significantly increasing depredation rates (Paluh et al. 2014, Bateman et al. 2017). If this strategy were applied in future studies utilizing models in the forest, we could obtain better estimates of predation rates that may more accurately reflect any effects of urbanization.

Snake models deployed were painted black to mimic a wide variety of water snake species found in the Great Trinity Forest. However, it is possible raptors interpreted these models as costly prey items since venomous water moccasins (*Agkistrodon piscivorous*) found in this forest are similar in color. Most predators make a post-detection decision on whether to attack prey based on developed search images of dangerous versus safe prey (Bateman et al. 2017). Due to instinctive avoidance of dangerous prey, it is plausible that mimics would not be depredated by raptors if other prey were available (Brodie 1993). This could have contributed to the low rate of raptor depredation we observed.

It is also important to point out that factors of urbanization affecting raptors and prey do not exist in isolation and results can change based on perspective. For example, prey hyperabundance generated from increased anthropogenic subsidies may occur simultaneously with an increase in the immigration of generalist raptors able to thrive in the same urban environment (Fischer et al. 2012, Boggie & Mannan 2014). If these raptors depredated these types of prey, the events may cancel each other out, indicating no detrimental effects of urbanization for either predator or prey species and therefore masking any disassociation in predator-prey relationships in the ecosystem.

While this study focused on the raptor community, it would be worthwhile to focus on individual species. For example, we recommended that future studies should focus on red-tailed and red-shouldered hawk foraging ecology and breeding performance given their high observed activity levels throughout the forest. Dietary habits, and predator-prey dynamics by extension, are strongly associated with breeding success and can differ between urban and rural environments due to prey availability and quality (Newton 1979, Kettel et al. 2008, Marzluff & Ewing 2001, Shochat et al. 2006). Breeding performance of species is routinely used as a measure of fitness for individuals and a proxy for habitat quality (Newton 1979, Preston & Beane 2009, Kettel et al. 2018). Many urban areas appear to contain viable habitat for raptors but are in fact population sinks (Kettel et al. 2018). That is, higher rates of successful fledglings have been observed in urban areas, but with a high rate of juvenile mortalities (Kettel et al. 2018). These mortalities are due to factors associated with urban areas such as disease, collisions with power lines and vehicles, poisonings, intentional shootings, etc. By linking species-specific feeding ecology, predator-prey dynamics, and reproductive success we will obtain better insight into raptor responses to urbanization and improve our assessment of the Great Trinity Forest's environmental health and ecosystem function.

The Great Trinity Forest has good potential for future urban predator-prey studies. Throughout the 10-week study period, we observed a robust raptor generalist population regularly across the forest. Other predators, specifically mesopredators, were diverse and frequently caught on field cameras. These predators included bobcats (*Lynx rufus*), coyotes (*Canis latrans*), raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and striped skunks (*Mephitis mephitis*). We also frequently encountered a wide variety of snake species including yellow-belled water snakes (*Nerodia erythrogaster*), diamondback water snakes (*Nerodia rhombifer*), banded water snakes (*Nerodia fasciata*), rough green snakes (*Opheodrys aestivus*), Western ribbon snakes (*Thamnophis sauritus*), Texas rat snakes (*Elaphe obsoleta lindheimeri*), copperheads (*Agkistrodon contortrix*), and water moccasins. Nonetheless, as an urban forest located within a highly populated area, other factors such as feral hogs, increased levels of noise, human presence, and habitat degradation and fragmentation were frequently observed.

There is still much unknown about urban trophic dynamics and food web linkages. Data collected from this study, combined with future recommended studies, will aid biologists in gaining a better understanding of urban predator-prey dynamics and raptor urban ecology within the Great Trinity Forest and other urban areas. This will increase the accuracy of predicted short- and long-term repercussions for both raptors and ecosystem functions. Gleaned knowledge will enable managers to identify key factors to aid in future urban and conservation planning. Measuring how raptor responses change as urbanization increases is necessary to quantify and mitigate any negative consequences to populations. Implementation of effective raptor management strategies will be essential to sustain healthy raptor populations with predictable encroachment of urbanization on historical natural habitats in the future.

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ABSTRACT

EVALUATING PREDATOR-PREY DYNAMICS IN AN URBAN FOREST: ASSESSMENT USING RAPTOR PREDATION ON PREY MIMICS

By Amber Renee Schenk, M.S., 2020

Department of Biology

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Thesis Advisor: Amanda Hale, Professor of Biology and Graduate Program Director

Predator-prey dynamics are fundamental in shaping and regulating wildlife communities; however, these relationships are often decoupled in urbanized areas. Our study sought to characterize raptor activity, depredation rates, and raptor-prey dynamics within the Great Trinity Forest, Dallas, TX. From May – August 2019, we conducted weekly raptor surveys and deployed prey mimics along an urban-to-rural gradient. We detected 161 raptors representing 8 species and found no relationship between raptor activity and degree of urbanization. However, when we examined urbanization as a categorical variable using our “high” and “low” sites, we found that raptor activity was significantly higher in the “low” sites. Of the 732 prey mimics deployed, 61 were attacked and we found no relationship with degree of urbanization. Furthermore, we found no relationship between raptor activity and depredations, suggesting that urbanization has no effect on raptor-prey dynamics within this forest or there is low raptor predatory response regarding prey mimics.