# Introduction

Urbanization is changing the face of our planet (Acuto et al. 2018). Not only do more people live in urban areas worldwide, but urban areas are also expanding at about twice the rate of their population size (Angel et al. 2011). This urban expansion, combined with an increasing urban population, drives global environmental change and threatens biodiversity worldwide (Grimm et al. 2008, Seto et al. 2012). And although a small percentile of Earth’s total land cover is classified as urban, the cumulative effects of urbanization on the planet are immense (Schneider et al. 2010). Thus, there is a great need to understand how urbanization influences Earth’s ecology and – possibly due to this need – rates of urban ecological research have dramatically increased in recent decades (Magle et al. 2012, Fidino and Magle, 2017, SOME OTHER REVIEW).

While urban ecological research is increasing, most studies occur within a single city which limits our understanding of urban ecosystems (Magle et al. 2019). While single-city research can, for example, identify how species respond to urbanization locally, it is difficult to extrapolate these findings to other cities that vary in age, cityscape structure, size, climate, or human population density (Aronson et al. 2016, Magle et al. 2019). Differences in land-cover and age between cities, for example, are correlated to differences in bird and plant richness (Aronson et al. 2014). Structural components that vary across cities can also influence population dynamics. For example, gene flow between populations of smaller, less motile species are reduced across water bodies within a city while other features such as railways facilitate gene flow (Beninde et al. 2018). As a result, the structural layout of a city influences where species may persist and can help or hinder movement between populations. Such patterns highlight how differences between cities influence wildlife population dynamics and therefore indicates that multi-city comparative approaches are necessary to understand how biodiversity responds to urbanization (Aronson et al. 2014; Beninde et al. 2018; Magle et al. 2019).

In this study we used data from the Urban Wildlife Information Network (UWIN) – a systematic multi-city biodiversity monitoring survey of urban green space – to quantify how differences between cities influence the distribution and relative occupancy of urban-adapted mammals throughout North America. Our goals were to determine if the relative occupancy or distribution of a species within a city changes as function of 1) the average housing density of a city and 2) how much habitat is available within a city. We predict that a species relative occupancy will decrease as the average housing density of a city increases but increase as the amount of habitat increases. Likewise, we predict that the magnitude of a species response to urbanization will be greater in more densely populated cities, but this relationship could be lessened in cities with more available habitat. We further previous multi-city biodiversity assessments by, for the first time, exploring whether the magnitude and direction of a species response to urbanization changes as a function of how a city is built. This unique approach therefore allows us to determine if results from a single-city generalize to other cities or if differences between cities result in distributional shifts of a species.

# Methods

## Site selection

Partnering UWIN cities follow a standard protocol to select sampling locations and monitor biodiversity, which is centered on the establishment of at least 25 sampling locations along spatial urbanization gradients (Magle et al. 2019; Figure 1). Sampling locations (hereafter sites) include an array of potential wildlife habitat in a city such as city parks, cemeteries, golf courses, natural areas, and backyards. Transects originate in the urban core of a city and travel outwards through suburban, exurban, and rural areas across varying levels of impervious cover and housing density. The average number of sites per city was 51 (min = 23, max = 104). Sites are located within 2 km of a transect – which generally follows a road, bike path, or natural feature like a river – and all sites are at least 1 km apart from one another. This 1 km distance was selected because it is greater than the radiuses of most city dwelling mammals, save for the coyote (*Canis latrans,* Gehrt et al. 2010). Likewise, many spatial covariates (e.g., impervious cover, housing density, etc.) from partnering UWIN cities are available at a 1 km spatial grain.

## Biological sampling

The current focus of UWIN has been passive monitoring of medium to large-sized mammals with motion-triggered trail cameras (hereafter camera traps). To do so, one camera trap is placed at a site four times per year for at least 28 consecutive days per deployment. Camera traps are placed roughly 1 to 1.5 m up from the ground on the trunk of a tree and angled in a downward trajectory towards another tree 2.5 – 6 m away. To potentially increase species detectability, a synthetic fatty acid scent (USDA Wildlife Services, Pocatello, Idaho) was placed in a mesh bag and nailed roughly 30 cm from the ground to the tree the camera trap was angled towards. To capture seasonality that may occur within a city, camera traps are deployed near the first day of January, April, July, and October each year. Some UWIN partners, however, sample continuously.

While UWIN currently has 23 partnering cities, a total of 10 cities had data that was available for this analysis, most of which comes from the July 2017 sampling season (Table 1). A few UWIN partners had data from multiple July sampling seasons, which we included in this analysis. Likewise, two UWIN cities (Long Beach, California and Wilmington, Delaware) only had data from July 2018.

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| Table 1. The number of sites with classified data per year and city. A dash indicates data was not available. | | | |
|  | Sites sampled and images completely classified | | |
| City | 2016 | 2017 | 2018 |
| Austin, Texas | - | 25 | - |
| Chicago, Illinois | 97 | 104 | 100 |
| Denver, Colorado | - | 40 | - |
| Fort Collins, Colorado | - | 31 | - |
| Iowa City, Iowa | - | 37 | 39 |
| Indianapolis, Indiana | - | 45 | 43 |
| Long Beach, California | - | - | 24 |
| Manhattan, Kansas | 74 | 74 | - |
| Madison, Wisconsin | - | 23 | 24 |
| Wilmington, Delaware | - | - | 28 |

At the time data was collected partners uploaded their camera trap photos into a modified version of the Colorado Parks and Wildlife Photo Warehouse database (Ivan and Newkirk 2016). Briefly, this distributed database allowed UWIN partners to link images from a deployed camera to a site, distribute images to experts for identification, and link image identifications to a site and camera deployment in a standardized relational database. A custom R package, *uwinr*, was used to check a cities respective database for errors and prepare data for analysis (Fidino 2017). For this analysis, we generated daily detection histories for each site and species. A detection history would take the value of 1 if a species was detected at a site on a given day. A value of 0 indicates a species was not detected on that day, and the value NA indicates that a camera was not deployed on a given day or it malfunctioned (e.g., batteries ran out). For example, the detection history {0, 0, 1, NA} indicates that a species was not detected on the first two days, detected on the third, and then either the camera malfunctioned or was removed on the fourth day. Detection histories were generated with a two-week buffer around each July sampling period to account for minor differences in deployment timings between cities.

## Statistical analysis

We fit hierarchical single-season single-species occupancy models to our data to estimate if the magnitude or direction of a species response to urbanization changed as function of structural differences between cities (MacKenzie et al. 2017). Four candidate models were fit to each species data. We explain the global model below. The remaining three models are simplifications of the global model.

In our global occupancy model, we included one within-city and two between-city spatial covariates. Our within-city covariate was the housing density around a site which was calculated as the thousands of housing units within 1 km buffer of a deployed camera trap (e.g., 2,500 units = 2.5). This term served as a proxy for the level of urbanization around a sampled habitat patch. For our first between-city covariate we used NLCD data to calculate the proportion of available green space within a city (CITATION). To do so, we first extended the width of each transect in a city by its respective length. A 20 km transect, for example, would become a square with 20 km sides wherein the transect line bisects the center of the square. Overlapping squares within a city were spatially joined to create each city’s sampled area. We then calculated proportion of available green space by combining the forest, herbaceous, shrub & grass, and low urban development land cover classes and dividing the area of those classes by the total sampled area (NLCD CITATION). For our second between-city covariate we calculated the average housing density across all sampled locations of a city. For example, the average housing density of Fort Collins, Colorado was calculated from its 31 sampled sites (Table 1). This covariate therefore represents the average housing density near greenspace within a city. Therefore, for a single species the logit-linear predictor of the probability of occupancy (*Ψ­js*) at *j* in 1,...,10 cities and *s* in 1,…,*Sj* sites is

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| --- | --- | --- |
|  |  | Eq. 1 |

where

|  |  |  |
| --- | --- | --- |
|  |  | Eq. 2 |

and

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| --- | --- | --- |
|  |  | Eq. 3 |

In Eq. 1, represents the average log-odds a species occupies a habitat patch in city *j*, which can vary as a function of our two between-city covariates – the average proportion of habitat in a city ( and the average housing density of a city (– via Eq. 2. These between-city covariates were centered and scaled to have a mean of 0 and a standard deviation of 1. is a slope-term that represents the relative log-odds change in occupancy at site *s* and city *j* given the within-city housing density covariate at site (i.e., the housing density within 1 km of a deployed camera). Furthermore, is group-mean centered by subtracting the respective city average . Scaling this way makes it easier to interpret the parameters in Eq. 2 and 3 (Aguinis et al. 2013). As with , we allow to vary in magnitude or direction via Eq. 3 based on our two between-city covariates. Moving back to Eq. 1, is a city-specific random effect. Finally, we account for multiple years of sampling at some cities with two indicator functions, and . The parameter is the log-odds difference in average occupancy at city *j* for sites sampled in 2016. Conversely, is the log-odds difference in average occupancy at city *j* for sites sampled in 2018 if and only if that city had 2017 data. For example, is separately estimated for the 2016 Chicago and Manhattan data but is zero otherwise (Table 1). Likewise, is estimated for the 2018 data of Chicago, Indianapolis, Iowa City, and Madison but not estimated for Long Beach or Wilmington because these two cities did not have 2017 data. For the detection model, we allowed a species probability of detection (*ρ*) to vary between cities such that the logit-linear predictor was where is the average log-odds of detecting a species while is a city level random-effect.

## Models, prior specification, and model selection

The four models we fit to each species data varied in the number of between city variables and represent different hypotheses about what structural differences between cities are correlated to how common a species is (via Eq. 2) or where they are most likely to occur within a city (via Eq. 3). The global model (*Mglobal*) contained both between city variables, the next model included the proportion of green space in a city (*Mhabitat*), the third model included the average housing density of a city (*Mhousing*), and the final model had neither of the between city variables (*Mnull*). All models included the measured housing density around each site (i.e., the one within-city variable) and the detection model did not differ between models. Furthermore, cities that were outside the distributional range of a species were omitted from that species analysis, and models were only fit to a species data if they were detected at a minimum of five UWIN cities.

We used a Bayesian framework to parameterize and evaluate our models. All logit-scale parameters save for the random effect terms were drawn from Logistic(0,1) distributions which represent a vague logit-scale prior. Random effects were drawn from N(0, σ) distributions where σ ~ Inv-gamma(0.001, 0.001). To compare the relative fit of each model we calculated the conditional predictive ordinate (CPO) of each data point along each step of an MCMC algorithm (Geisser 2017). Overall model performance was evaluated with the summary statistic for data point *k* and MCMC step *t* and the lowest value indicates the best relative fit (Hooten and Hoobs 2015). Models were fit in JAGS (Plummer 2003) version 4.3.0 (Plummer 2003) via the R programming language version 3.5.3 (R Core Team 2019). After a 60,000 step adaptation and 60,000 step burn-in each model was sampled 1,250,000 times across 5 chains. Chains were thinned by 10 for a total of 125,000 samples due to the computational intensity of tracking the CPO of each data point. To verify model convergence, we ensured that Gelman-Rubin diagnostics for each parameter were < 1.10 and looked at trace plots of parameters from the MCMC chains (Gelman et al. 2014). While the number of parameters is different for the best-fit model of each species, we reference parameters as we did for the global model (i.e., Eq. 1 – 3) for consistency.

# Results

A total of 25,115 camera trap nights occurred across 808 camera deployments at 569 sites in 10 UWIN cities. Eight species had enough data to analyze, which represent a common suite of urban adapted medium to large mammals throughout North America. In order of most to least detected, this included the raccoon (*Procyon lotor*, 5504 detections), eastern gray squirrel (*Sciurus carolinensis*, 2465 detections), Virginia opossum (*Didelphis virginiana*, hereafter opossum, 2210 detections), eastern cottontail rabbit (*Sylvilagus floridanus*, hereafter e. cottontail, 1731 detections), fox squirrel (*S. niger*, 1508 detections), coyote (*Canis latrans*, 821 detections), striped skunk (*Mephitis mephitis*, 548 detections), and red fox (*Vulpes vulpes*, 368 detections). Species were detected in an average of 8.25 cities. Gray squirrel were detected across the fewest number of cities (n = 6), while raccoon were detected in all 10 cities.

Model selection results indicated that structural differences between cities influenced the within-city habitat dynamics of all but one species, the striped skunk (Table 2). Skunk had an average occupancy of 15.26% (95% CI = 10.56 – 20.53, Figure 1a) across cities with little between-city variability (σskunk = 0.14, 95% CI = 0.01 – 0.55). Skunk responded negatively to site-level housing density, which indicates that skunk were more likely to occupy habitat patches away from dense human populations, and this relationship did not differ between cities (Figure 1b). For example, a 1,000 unit increase from a cities average housing density decreased skunk patch occupancy by roughly 5% to 10.89% (95% CI = 6.71 – 16.29).

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| Table 2. Model selection results of the four candidate models fit to each species data. Models were compared with the summary statistic for data point *k* and MCMC step *t*, where CPO is the conditional predictive ordinate. Lower values indicate better model fit. The lowest score, which represents the best fit model, is bolded for each species. Species are sorted by their best fit model. | | | | |
| Species | *Mglobal* | *M­housing* | *Mhabitat* | *M­null* |
| gray squirrel | **2128.28** | 2131.34 | 2128.63 | 2129.17 |
| coyote | 1211.06 | **1209.59** | 1210.46 | 1215.48 |
| opossum | 2205.11 | **2204.39** | 2204.95 | 2205.8 |
| raccoon | 4400.48 | **4399.26** | 4401.09 | 4400.87 |
| e. cottontail | 1962.64 | 1962.4 | **1961.38** | 1961.93 |
| fox squirrel | 1610.9 | 1612.69 | **1610.11** | 1632.01 |
| red fox | 547.87 | 548.47 | **547.82** | 549.79 |
| striped skunk | 915.158 | 913.63 | 913.881 | **911.55** |



Figure . Between-city effects from the top model of each species. The left plot (a) illustrates the average log-odds a species occupies a habitat patch within a city and how that may change due to structural differences between cities. The right plot (b) demonstrates the magnitude and direction of a species response to site-level housing density within a city and how that may change due to structural differences between cities. Parameters are on the logit scale which are reported from the best-fit model of each species.

## Changes in relative occupancy due to structural differences between cities

The relative occupancy of raccoon and e. cottontail were influenced by structural differences between cities (Figure 2a). Raccoon relative occupancy was highest in cities with lower than average housing density and lowest in cities with higher than average housing density (Figure 2a, -0.58, 95% CI = -1.18 - -0.01). Overall, raccoon had the highest average relative occupancy compared to other species (i.e., had the most positive intercept estimate, Figure 1a). Conversely, there was some evidence that e. cottontail relative occupancy decreased in cities with less habitat (Figure 2b, = -0.22, 95% CI = -0.49 – 0.03).



Figure 2. The within-city relative occupancy of (a) raccoon changes depending on how densely populated a city is while (b) eastern cottontail relative occupancy decreases in cities with less habitat. Solid horizontal lines are mean model predictions of a species relative occupancy in a city while shaded ribbons are 95% credible intervals of this prediction. Gray dots represent city-specific occupancy estimates for the UWIN cities that detected the species while vertical bars are 95% credible intervals. Raccoon (a) had more between city variability from the mean predicted response than eastern cottontail (b).

There was less evidence that the within-city relative occupancy of other species changed as a function of a city’s proportion of habitat or average housing density. The relative occupancy of red fox, gray squirrel, and fox squirrel may increase in cities with more habitat, but 95% credible intervals of these estimates greatly overlapped zero (Figure 1a). Likewise, opossum may become less common in cities that are more densely populated, but the estimated difference between cities was small (= -0.14, 95% CI = -0.46 – 0.28, Figure 1a). Coyote relative occupancy likely does not differ between cities ( = 0.02, 95% CI = -0.23-0.28), which indicates that coyote occupy about 38.39% (95% CI = 31.23 – 45.35) of urban green space within a city regardless of structural differences.

## Changes in response to urbanization due to structural differences between cities

The effect of site-level housing density on the patch occupancy of fox squirrel, gray squirrel, and red fox changed as a function of the proportion of habitat in a city (Figure 1b). For example, if the proportion of habitat in a city was less than 19.70% (95% CI = 16.90 – 22.69%; Figure 3a) fox squirrel responded negatively to urbanization and were therefore less likely to occupy habitat patches surrounded by above average levels of housing density within a city. Conversely, fox squirrel responded positively to urbanization if the proportion of habitat in a city was greater than 19.70% and were then more likely to occupy green space surrounded by above average levels of housing density. Gray squirrel and red fox followed a similar pattern to fox squirrel and both species responded positively to urbanization in cities that had a higher proportion of habitat (Figure 3b-c).



Figure 3

The effect of site-level housing density on the patch occupancy of coyote, opossum, and raccoon changed in cities with different average housing densities (Figure 1b). Opossum and raccoon responded negatively to urbanization in densely populated cities and were therefore less likely to occupy green space within a city surrounded by higher levels of housing density (Figure 4a-b). For example, Chicago, Illinois had the highest average housing density in this analysis (1316.70 houses km-1) and there was strong evidence raccoon and opossum negatively responded to site-level housing density ( = -0.55, 95% CI = -0.77 – -0.35; = -0.56, 95% CI = -0.80 – -0.33). Conversely, raccoon and opossum may respond positively to urbanization in cities with a lower average housing density (Figure 4a-b). For instance, Manhattan, Kansas had the lowest average housing density in this analysis (313.35 houses km-1) and there was some evidence raccoon and opossum responded positively to site-level housing density ( = 0.41, 95% CI = -0.34 – 1.18; = 0.27, 95% CI = -0.37 – 0.92). Therefore, the spatial arrangement of raccoon and opossum varied depending on how densely populated a city was. Coyote, however, always responded negatively to site-level housing density within a city but the strength of this effect was reduced more densely populated cities (Figure 4c). Thus, while coyote were most likely to be found in urban green space away from people, this relationship was strongest in sparsely populated cities.

## Differences in within and between city species richness

Using posterior simulations of species occurrences from each species best-fit model we calculated 1) within-city species richness in urban green space surrounded by less than or more than a city’s average housing density 2) the most likely community to occur at the estimated median species richness (Figure 5). Across cities, urban green space with less than average housing density had an average of 3 mammals while urban green space with more than average housing density had 2.6. For cities with more than 750 houses km-1 on average, species richness was lower in habitat patches surrounded by greater than average housing density (Figure 5). The species that was most often lost from the community was the raccoon. For cities with less than 750 houses km-1 on average, within city differences in species richness were unequivocal. Raccoon was the most common species to be observed in a wildlife community while the skunk was the least.

## Discussion

Urban ecologists – following historical urban growth models – initially assumed urban areas decreased in density by radial concentric circles from their urban core outwards, like an onion (McDonnel and Pickett 1990). As a result, urbanization was measured as Euclidean distance to a city center (McDonnel and Pickett 1990). Cities today, however, are often polycentric and therefore do not follow this pattern. This, in turn, has required more robust measures of urbanization (CITATION). Examples include … Despite the chosen metric for urbanization,

because edge cities along the periphery of major metropolitan areas

Traditional models of urban growth and subsequent ecological explorations or urban environments were monocentric and assumed urban areas decreased in density in radial concentric circles from their urban core outwards (McDonnel YEAR). Yet, most cities today do not follow such a pattern, as edge cities along the periphery of major metropolitan areas grow.

habitat loss (CITATION),

drive global environmental change (Grimm et al. 2008), and threaten biodiversity worldwide (Seto et al. 2012). This is an impressive feat given that currently only a small percentile of Earth’s total land cover is classified as urban

– the process where the built environment is created to accommodate urban populations and their activities –

And though a small percentile of Earth’s total land cover is classified as urban (CITATION) their influence on glob

The process of urbanization significantly alters ecological processes (CITATION) and threatens biodiversity worldwide (CITATION). Though on

The face of the planet has not only been changed by urbanization (Acuto et al. 2018), but more people live in cities today than ever before (CITATION).

Urbanization is changing the face of our planet (Acuto et al. 2018). On average,

Urbanization – the process where the built environment is created to accommodate urban populations and their activities – occurs at twice the rate of population growth on average (Angel et al. 2011).

Though urban areas Urbanization is changing the face of our planet (Acuto et al. 2018). Though only 10% of the Earth’s total land surface area is classified

To accommodate the current human migration from rural environments to cities has resulted in increased rates of urbanization worldwide (Citation), which in turn si

To meet the demands of an ever-growing urban population, urbanization rates have increased worldwide. only 10% of the Earth’s

The process of urbanization is changing the face of our planet (Acuto et al. 2018). While only 10% of the Earth’s total land surface area is classified as urban (McGranahan, 2005) over 50% of the world’s population now resides cities (CITATION). The migration of humans into cities continues to increase rates or urbanization (CITATION), significantly alter ecological processes (CITATION), and threaten biodiversity worldwide (CITATION). As a result,

With a growing urban population rates of urbanization continue to increase worldwide (CITATION). Consequently, lands of conservation value that were once safely outside a city’s boundary are often become ingrained within a spreading urban landscape and are typically diminished in size (CITATION).

In fact, the cumulative effects of urbanization is transforming the ecology of our planet.

With the expansion of cities protected areas become ingrained within an urban

**Discussion**

As predicted,

species richness in a city changed as a city becomes more densely populated . Species richness in sparsely populated cities either increased, decreased, or stayed the same with increasing urbanization (Figure X). In densely populated cities, however, species richness unequivocally decreased with increasing urbanization, and this shift occurred once a city had ≥ 900 houses km-1 (Figure X).

A few species likely caused this difference. Raccoon, for example, are found in different parts of a city depending on how densely populated it is. In less densely populated cities, raccoon respond positively to urbanization and are more likely to be found in habitat patches surrounded by more houses (FIGURE Y). The opposite is true in densely populated cities ­ – raccoon are more likely to be found in habitat patches surrounded by fewer houses. When combined with their relatively high average occupancy across cities (NUMBER)

Raccoon, for example, become far less common

1. Urbanization is a big and important thing
2. Study along gradients has been fruitful for ecological research.
   1. ‘simpler gradients’ such as impervious cover, housing density
   2. Socio-economic potentially reveal other issues.
3. However, cities are not identical to one another, and therefore revealing trends along an urbanization gradient of one city may not translate to another.
   1. Some of the potential reasons
   2. These differences BETWEEN cities may therefore cause rise to observed differences in how common a species is or where it is located WITHIN a city
   3. The only way to explore this idea is to study gradients OF cities instead of a gradients within a single city.
4. UWIN is a way to answer questions at this scale.
   1. Large-scale and systematic survey, wherein partners follow a common study design (Magle et al. 2019).
   2. The goal of this study was to determine if (1) how densely populated a city is and (2) how much available green space within a city influences how common different species are or where they are located within a city.
   3. We predict that in densely populated cities, wildlife species would become less common and that they would be located within less densely populated portions of a city. Likewise, we predict that wildlife in cities with more greenspace would become more common (observed in more habitat patches) and that this could potentially allow species to be located within more densely populated portions of a city (WHY DO WE REALLY THINK THAT).

METHODS

Study sites

1. (Look at Magle paper and briefly cover this). Maybe talk to Travis about putting together a map that shows the sites but with a housing density layer instead of NLCD data?

Data collection

1. Cameras placed 4 times a year in January, April, July, and October.
2. Put on a tree roughly 1.5 meters from ground, angled in a downward facing direction towards a scented lure nailed to another tree roughly 0.1 meters from the ground.
3. Some cities included data from additional years (maybe a table?)
4. 8 species included in the analysis? DO WE REMOVE ANY?

Analysis

1. Single-season occupancy model
2. To explore differences within and between cities, we used group-mean centering of our single within-city variable.
   1. Math it
   2. Explain why it is useful
3. Write out the model with some math
4. Bayesian framework, lots of iterations, checked for convergence

Results

Discussion

Come up with some really cool unifying remarks about what an analysis of this type teaches us about urban ecology, and steps moving forward.

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