# Abstract

TDB (Shooting for 150 words), will work on after discussion written.

# Introduction

Urbanization is changing the face of our planet (Acuto et al. 2018). For the first time ever, more people live in urban than rural areas worldwide, and to meet this demand, urban areas are 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 percentage of Earth’s total land cover is classified as urban, the cumulative effects of urbanization on the Earth’s biodiversity 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 between cities (Aronson et al. 2014). Structural components that vary across cities can also influence where such species may persist and can help or hinder movement between populations. Gene flow between populations of less motile species, for example, are reduced across water bodies within a city while features such as railways facilitate gene flow (Beninde et al. 2018). 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) how much habitat is available within a city and 2) the average housing density of a city. We predict that a species relative occupancy will increase as the amount of habitat increases but decrease as the average housing density of a city increases. Likewise, we predict that the magnitude of a species response to urbanization, which defines their distribution in a city, will be most negative 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

UWIN partners follow a standard protocol to select sampling locations which is centered on the establishment of at least 25 sampling locations along spatial urbanization gradients (Magle et al. 2019). Sampling locations (hereafter sites) include an array of potential wildlife habitat 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 gradients 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 follow a road, bike path, or natural feature like a river. All sites are separated by at least 1 km. This 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).

## 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 1 to 1.5m from the ground on the trunk of a tree and angled in a downward trajectory at another tree 2.5 – 6m away. To potentially increase species detectability, a synthetic fatty acid scent tablet (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 in wildlife distributions 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, 10 had data available for this analysis, most of which comes from the July 2017 sampling season (Table X). These cities are Austin, Texas; Chicago, Illinois; Denver, Colorado; Fort Collins, Colorado; Iowa City, Iowa; Indianapolis, Indiana; Long Beach, California; Manhattan, Kansas; Madison, Wisconsin; and Wilmington, Delaware. 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 X. 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 these data were collected, partners uploaded their camera trap photos into a distributed Access database built for camera trapping research (Ivan and Newkirk 2016). Briefly, this 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, species, and sampling season. A detection history took the value of 1 if a species was detected at a site on a given day, the value 0 if a species was not detected on that day, and the value NA if the camera malfunctioned (e.g., batteries ran out) or the camera was not deployed on a given day. 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 reduced versions of our 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 a 1 km buffer of a deployed camera trap (e.g., 2,500 units km-2 = 2.5). This term served as a proxy for the level of urbanization around a site. For our first between-city covariate we calculated the proportion of available green space within a city. To do so, we first extended the width of each transect in a city by its respective length. A straight 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 crated from multiple transects within a city were spatially joined to create each city’s sampled area. We then calculated the proportion of available green space in a city by combining the forest, herbaceous, shrub & grass, and low urban development land cover classes from the National Land Cover Database and divided 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 sites of a city. For example, the average housing density of Fort Collins, Colorado was calculated as the mean housing density of its 31 sampled sites (Table X). This covariate therefore represents the average housing density near greenspace within a city. 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

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|  |  | Eq. 2 |

and

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|  |  | Eq. 3 |

In Eq. 1, represents the average log-odds a species occupies any habitat patch in city *j*, which can vary as a function of our two between-city covariates – the 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 so the parameters in Eq. 2 and 3 represent between-city effects (Aguinis et al. 2013). As with , we allow to vary in magnitude or direction via Eq. 3 as a function of 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 and is otherwise zero (Table X). 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 comparison (Table X). 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 fit to each species data differed in the number of between-city variables and represent separate hypotheses about which 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. Due to the computational intensity of tracking the CPO of each data point, chains were thinned by 10 for a total of 125,000 samples. 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 to ensure proper mixing (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 from 808 camera deployments at 569 sites across 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 1). 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. 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), no matter what the average housing density of a city was.

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| Table 1. 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 best-fit 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.

## 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 a low average housing density and lowest in cities with a high 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., 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 between cities.

## 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%) 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 (Figure 3a). Conversely, fox squirrel responded positively to urbanization if the proportion of habitat in a city was greater than 19.70% (Figure 3a). 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 within-city response to urbanization, as represented by site-level housing density km-2, of (a) fox squirrel, (b), red fox, and (c) gray squirrel changes in magnitude and direction as a function of how much habitat is within a city. Solid horizontal lines are mean model predictions of a species response to urbanization in a city while shaded ribbons are 95% credible intervals of this prediction.

The effect of site-level housing density on the patch occupancy of coyote, opossum, and raccoon changed as a function of average housing density (Figure 1b). Opossum and raccoon responded negatively to urbanization in densely populated cities (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 responded negatively 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 distribution of raccoon and opossum within a city 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 in 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.



Figure 4. The within-city response to urbanization, as represented by site-level housing density km-2, of (a) raccoon, (b), opossum, and (c) coyote changes in magnitude and/or direction as a function of the average housing density of a city. Solid horizontal lines are mean model predictions of a species response to urbanization in a city while shaded ribbons are 95% credible intervals of this prediction.

## 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 and 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 710 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 wildlife community was the raccoon. For cities with less than or equal to 710 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.

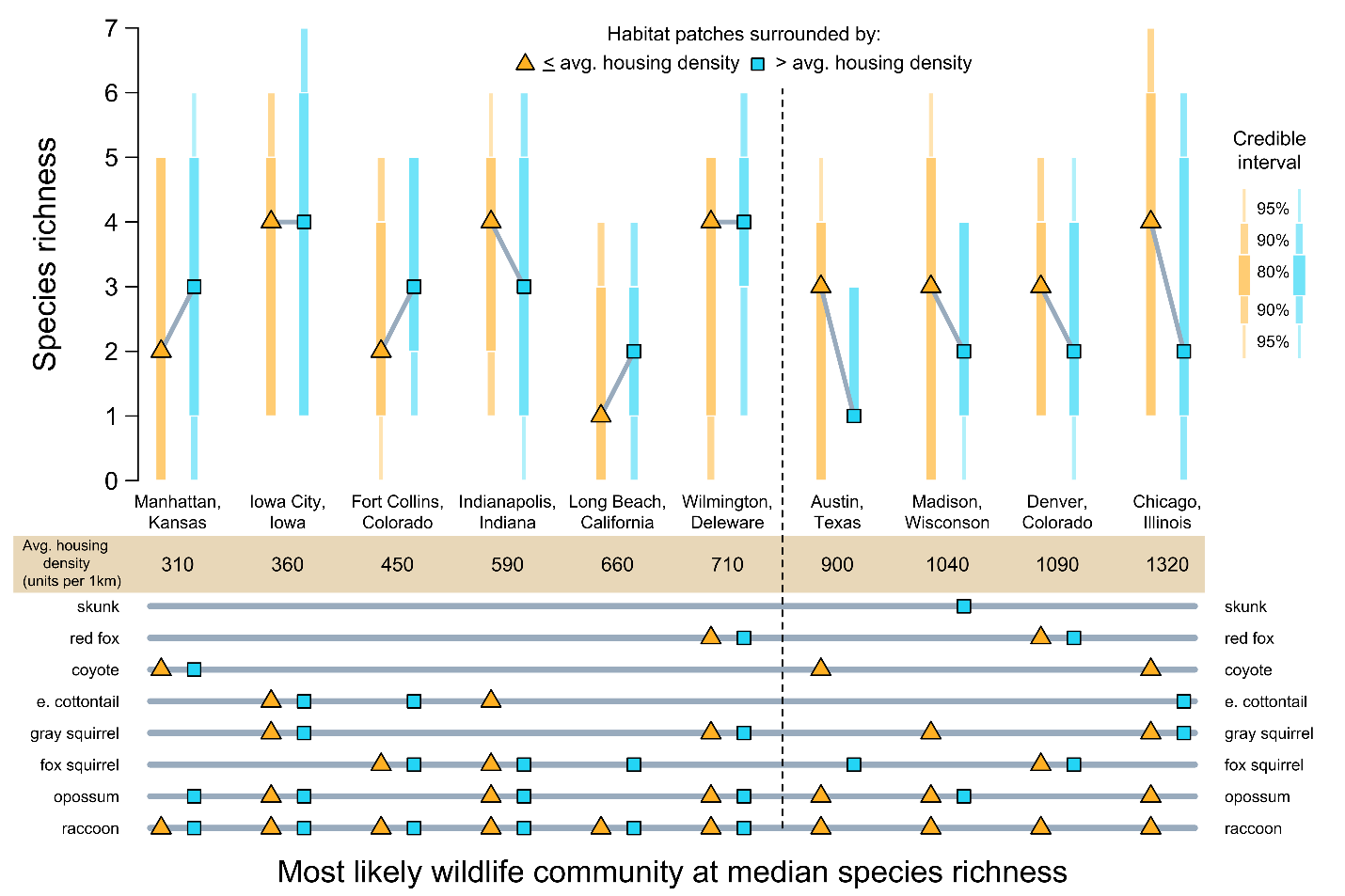


Figure 5. A comparison of the estimated species richness to urban green space surrounded by less or more than the average housing density of a city. Cities are ordered from left to right, lowest to highest, by average housing density. The lower plot represents the most likely wildlife community at the median estimated species richness at urban green space in a city surrounded by less than or more than the average housing density of a city. The vertical dotted line represents an apparent shift in differences between species richness: cities with an average housing density > 710 houses km2 always had fewer species in habitat patches surrounded by dense human populations.

# Discussion

1. **Key takeaways from our analysis (i.e., revisiting our predictions)**
   1. Biggest result. 7 or the 8 species responded to ‘urbanization’ differently depending on some between-city variable. Not only does the magnitude of effect change, but ALSO THE DIRECTION for some species. This has some very large and unifying implications for urban ecological research. A species ‘does not simply’ respond to urbanization, but the structure of the urban environment has an influence on how they respond. Some cities have red fox downtown, others do not.
   2. Bigger result. The relative occupancy of some species changes (e.g., rabbits and raccoon). Some species have raccoon everywhere (e.g., Indianapolis), other cities do not.
   3. Big result. The relative occupancy of other species does not (i.e., we can generalize). This is more for the skunk and partly the coyote.
2. **Revisiting our predictions (More specifically).**
   1. Yep, most species responded negatively to between-city housing density, most species responded positively to habitat (at least with response to site level urbanization). Coyote was a weird one, likely because their home range increases in REALLY urban areas.
   2. Habitat, for the most part, decreases the negative influence of urbanization. More habitat = species found further into a city. Did not occur with cottontail rabbit (predators or something)?
3. **What these results mean to the literature.**
   1. It should not be surprising that species respond differently to the form and function of a city. In fact, this clearly spells out an opportunity: cities could be constructed in such a way to reduce the negative influences of urbanization on wildlife.
   2. More green space also positively influences people! It’s a win-win.
   3. Stop categorizing ‘urban’ all willy nilly! These results REALLY indicate that we need to look at quantifiable measures of urbanization and not categories because what is considered ‘urban’ greatly varies between cities.
   4. Species have often been couched into terms such as urban avoiders, exploiters, etc. However, it is not so much about a species adaptability to urban environments, per se, so much as the structure of the urban environment.
   5. As most research is from a single city, it was necessary that most research focuses on within-city factors that influence wildlife. Yet, the magnitude and possibly the direction of these within-city effects can vary based on large scale (between-city elements). We need to encourage researchers to consider why they observed differences in a broader sense. If we conducted our study in silos, some cities would find a species responds positively to urbanization while other see that they respond negatively. Only by bringing our data together do we actually see the pattern that arises and can start making generalities both within and between cities. THIS MOVES US TO…
4. **The role of multi-city, collaborative, research.**
   1. Has proven necessary to advance many ecological fields
   2. Urban ecology is likely no different. As more cities join UWIN, and we generate additional data, this analysis can represent a way to generate testable predictions for what should be expected in a city given our current knowledge on the habitat dynamics of these species both within and between cities.
   3. This is the next big step for our field, and will require a lot of (SOMETHING).
5. **Conclusion.** 
   1. Very brief recap.
   2. Our analysis is the first of its kind to explore these types of dynamics for wildlife. As researchers, this indicates we must more critically consider the environment (i.e., the city) when discussing results. As conservationists, this indicates that more habitat can partially decrease the negative influence of urbanization, and for some species actually make them more likely to live near people.
   3. Come up with some really cool unifying remarks about what an analysis of this type teaches us about urban ecology, and some final steps moving forward!

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