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Research Article

Thinking outside the park: recommendations for camera trapping mammal communities in the urban matrix

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Abstract

Urbanization is increasing globally, fragmenting habitats and prompting human–wildlife conflict. Urban wildlife research is concurrently expanding, but sampling methods are often biased towards large and intact habitats in public green spaces, neglecting the far more abundant, but degraded, habitats in the urban matrix. Here, we introduce the *Five P's of Urban Ecology*—Partnerships, Planning, Placements, Public participation and Processing—as a path to overcoming the logistical barriers often associated with camera-trapping in the urban matrix. Though the *Five P's* can be applied to a variety of urban sampling methods, we showcase the camera-trapping efforts of the DC Cat Count project in Washington, DC, as a case study. We compared occupancy models for eight urban mammal species using broad categorizations of land cover and local land use to determine drivers of mammal occurrence within the urban matrix as compared with urban habitat patches. Many native species maintained a strong association with large, semi-natural green spaces, but occupancy was not limited to these locations, and in some cases, the use of private yards and the built environment were not notably different. Furthermore, some species exhibited higher occupancy probabilities in developed areas over green spaces. Though seemingly intuitive, we offer advice on how to greatly reduce habitat-biased sampling methods in urban wildlife research and illustrate the importance of doing so to ensure accurate results that support the formation of effective urban planning and policy.

Key words: camera traps, urban ecology, urban matrix, mammals, occupancy

Introduction

Since 1970, the study of urban wildlife has become increasingly common (Magle et al. 2012), partially due to the advancements of noninvasive camera traps to document the distribution and behavior of diverse urban taxa (Caravaggi et al. 2017; Anton et al. 2018; Magle et al. 2019). Camera traps collect wildlife images and record pertinent metadata such as the date, time and locations of observations, without the negative effects of human presence and allow for collection of reliable data on elusive, rare, and nocturnal species (McShea et al. 2016). To date, several studies have investigated urban mammal communities, often documenting unprecedented levels of diversity across anthropogenic landscapes and uncovering unexpected urban animal interactions (Gallo et al. 2017; Mueller et al. 2018; Parsons et al. 2018; Mowry and Wilson 2019).

Though there are numerous methods of classifying urban areas, a review of urban wildlife literature revealed that most research defines a site's degree of urbanization by its surrounding structures (Moll et al. 2019). Sanwick et al. (2003) propose that the urban structural landscape can be broadly categorized into buildings and the space around them, called the external environment. The external environment comprised gray or green space, defined by the prevalence of impermeable surfaces. Both gray and green space can be further classified by its function rather than structure (Fig. 1). Under this system, many locations can be classified as green space despite vastly different land management. For instance, cemeteries and forest preserves are both considered green space under this definition. While both support wildlife, they differ in the quality of habitat and the species composition (Gallo et al. 2017). Since the function and structure of urban green spaces can vary broadly, using a binary system to classify urban spaces as green or gray imposes limitations on our understanding of urban ecosystems. This limitation can be addressed by studying urban wildlife populations through the lens of landscape ecology, which contextualizes the biodiversity in habitat patches by exploring habitat connectedness.

In their foundational research of landscape ecology, Forman and Godron (1981) describe habitat patches as areas of similar structural habitat surrounded by a dissimilar structural habitat, referred to as the matrix. Patches may be isolated within the matrix or connected by corridors that facilitate the movement of species between patches (Forman and Godron 1981; Turner 1989). In areas altered by anthropogenic development, habitat patches are typically associated with semi-natural spaces, or spaces with little human development relative to the surrounding environment (Krosby et al. 2015). Since the green space that surrounds these patches, such as drainage ditches or hedgerows, may share structural similarities with the larger patches they connect, they have the potential to operate both as corridors and habitats (Forman and Godron 1981). Through this lens, we propose that urban habitat patches and corridors be described as large or linear patches of similarly structured urban green space that sustain populations of wildlife (e.g. large parks and nature reserves), and the urban matrix is the surrounding, dissimilar, and often developed, environment. While the urban matrix includes features such as roads and alleys, it also includes green space that is not traditionally considered habitat for many species, such as residential yards, landscaped medians and vacant lots (Fig. 2).

Many urban wildlife studies focus on such habitat patches and corridors (Hegglin et al. 2004; George and Crooks, 2006; Roberts et al. 2006; Cove et al. 2012; Chupp et al. 2013; Saito and Koike, 2013; Schuette et al. 2014; Wang et al. 2015; Jones et al. 2016; Ehlers Smith et al. 2018; Moll et al. 2018, 2020; Schmid et al. 2018; Gallo et al. 2019; Mowry and Wilson, 2019). However, the departure of individuals from patches and corridors into the matrix is a documented behavior in non-urban systems (Baguette and Van Dyck 2007; Revilla and Wiegand 2008), suggesting that structural patch connectivity is not necessarily indicative of functional patch connectivity (Berger-Tal and Saltz 2019). It is reasonable to assume that, to some extent, wildlife occupancy in the urban matrix exists as well; however, few studies have investigated this directly (Kays and Parsons 2014; Schmid et al. 2018; Dorning and Harris 2019; Parsons et al. 2019). Studying how species use the urban matrix can offer insight into the differences between urban structural and functional

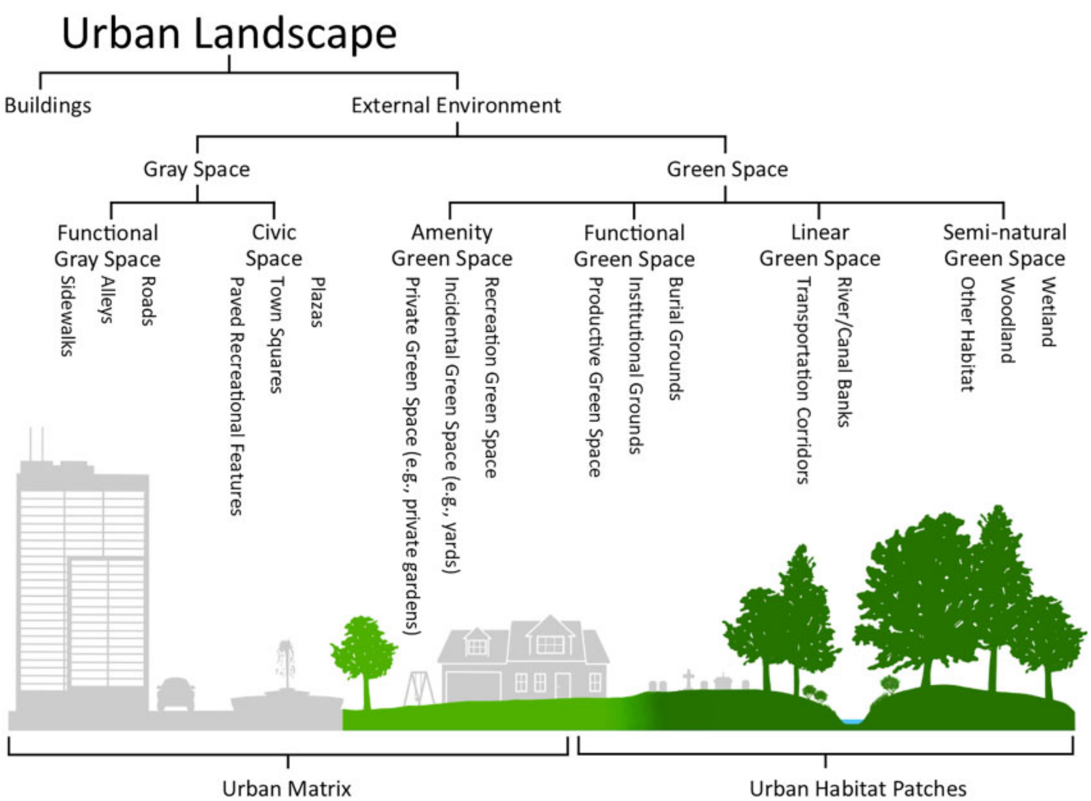

Figure 1: Diagram of the urban landscape classifications as proposed by Sanwick et al. (2003). Dark green land indicates landcover traditionally considered urban habitat, while light green land indicates green space not traditionally considered habitat. Some overlap exists between these categorizations depending on the city, and the physical structure of the landcover. Gray indicates impervious surfaces and buildings.

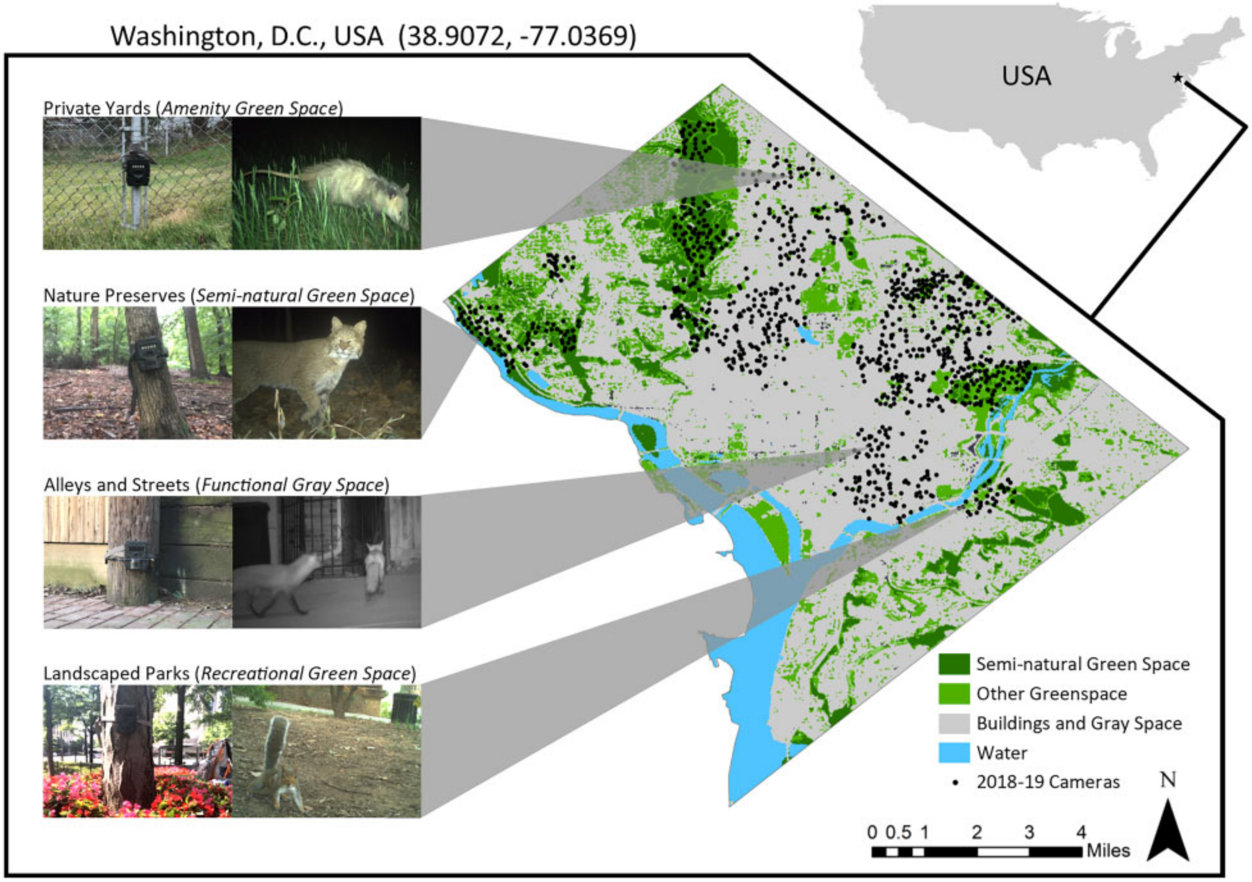

Figure 2: Camera traps deployed across Washington, DC (2018–2019) in both gray space and green spaces with accompanying photos of four different deployment types and the resulting wildlife observations: Virginia opossum (*Didelphis virginiana*) from a private yard, bobcat (*Lynx rufus*) from a semi-natural green space, red foxes (*Vulpes vulpes*) from an alley, and eastern gray squirrel (*Sciurus carolinensis*) from a public park.

connectivity and potentially inform conservation-minded urban planning. Despite the opportunity for such gains, urban ecologists often focus their sampling efforts in habitat patches rather than the matrix, especially when using camera traps. Even when studying species that maintain a strong association with heavily developed areas and human population density (e.g., domestic cats [*Felis catus*]), previous research has largely focused on sampling large public green spaces (Bengsen et al. 2011; Cove et al. 2018; Hansen et al. 2018) or radio-collared individuals (Gehrt et al. 2013; Hanmer et al. 2017; Kays et al. 2020a), rather than using camera traps to sample the urban matrix, where domestic cat occurrence is presumably highest.

Restricting urban ecological research to large patches of green spaces is problematic for multiple reasons. Importantly, this sampling strategy excludes the most abundant land uses of urban areas (Cerra 2017; Dyson et al. 2019). Thus, our knowledge of the ecological processes in a land cover that poorly represents urban areas is imposed upon the rest of the ecosystem, potentially leading to biased inferences about urban wildlife populations and ill-informed wildlife policy (McCance et al. 2017). This limited approach obscures differences in species' responses to urbanization and the implications these responses may have on future urban planning (Cove et al. 2019). For example, exclusive sampling of sizable urban habitat patches may lead to the false assumption that all species detected are equally suited to live in urban areas, whereas additional sampling in the matrix could reveal species-specific differences in dispersal ability and thereby differences in their resiliency to disturbance and habitat fragmentation. Additionally, research that disproportionately studies wildlife in relatively large urban green spaces may contribute to the misconception that wildlife 'belong' exclusively in these spaces, unintentionally portray animals outside of parks as unwelcome (McCance et al. 2017; Hunold 2019). Finally, disproportionate sampling in urban green spaces may not adequately reflect some of the ecological impacts of urbanites themselves. Cities foster a patchwork of human densities and cultures, and the resulting ecological landscape can be as diverse as the social landscape that drives it. Household factors such as resident lifestyle and family demographics, housing age, socioeconomic status, and geographic position in the urban matrix itself have all been found to impact local vegetative cover (Grove et al. 2006; Knapp et al. 2012; McPhearson et al. 2013; Ehlers Smith et al. 2018; Fernández et al. 2019; Schell et al. 2020), which likely influence wildlife communities and their trophic interactions (Faeth et al. 2005; Evans et al. 2017). Though these factors can be included as landscape variables for studies within relatively large green spaces such as parks, Moll et al. (2020) suggest that species-specific responses to urbanization may be lost if the scale of the variable is not proportional to the scale of the species' response.

Beyond gaining an understanding of the impacts of heterogeneous human-driven factors (e.g. differences in landscaping along a single city block) on wildlife, sampling the urban matrix offers social benefits as well. Urban residents are increasingly disconnected from the nature, but including urban residents in environmental research can lead to increased knowledge of and care for the natural world by creating opportunities for informal science education (Bonney et al. 2009; Schuttler et al. 2018). Studies that engage volunteers in data collection pertaining to wildlife found that participants show an increase in scientific literacy and a greater awareness of the species or ecosystems that they helped monitor (Brossard et al. 2005; Mitchell et al. 2017). In a literature review of the outcomes of public participation in ecological research, Schuttler et al. (2018) identify that most participants report having an interest in nature prior to their involvement in research, and call for the intentional involvement of those who do not already share this view. Sampling private residences presents a possible path to achieve this by offering residents who may not be interested in ecology an opportunity to participate in environmental research that does not require significant investment of their time or resources.

Nevertheless, sampling the urban matrix presents a unique set of challenges, including obtaining permission to work on private land, regularly interacting with the public, collecting an abundance of non-animal photographs, and equipment theft or damage. These challenges often discourage ecologists from conducting research in the urban matrix, especially if they are new to the field of urban ecology (Dyson et al. 2019). However, these barriers can be overcome by using what we term the *Five P's of urban ecology*, which include partnerships, planning, placements, public participation and processing. Though this approach may seem intuitive, we have found mindful adherence to these principles yields a successful sampling strategy and is beneficial for both researchers and the public. Here, we give a broad overview of the *Five P's* and showcase their application in a case study from the DC Cat Count, a survey of free-roaming cats and urban wildlife throughout Washington DC.

Partnerships

Ownership of urban land is split amongst numerous parties, necessitating a network of partnerships to adequately sample the urban matrix. Local institutions typical in governments, such as departments of transportation, libraries and fire and police departments, are all organizations grounded in the community—making them helpful partners. Such organizations are likely to own or manage multiple properties across the urban matrix, which can provide researchers with access to a wealth of sampling sites under one agreement. Partnering with homeowners and local businesses in the areas between institutionally owned properties can ensure adequate coverage of the entire urban matrix.

Private land is typically highly accessible, and cameras left on private lands are generally less likely to be disturbed or stolen than cameras left on public land (Dyson et al. 2019). However, establishing private partnerships often requires a different approach than is needed to establish public partnerships. Targeted outreach to institutions, businesses and residents is often as time-consuming as it is necessary. A variety of methods can be used to engage residents, including cold calls, community newsletters, community meetings, direct mail/canvassing or by posting a link to sign up via social media. We have found social media and cold calls to be the most productive methods for engaging residents, while the remaining methods of contact brought mixed success. Leaving informational flyers in residential neighborhoods yielded the fewest residential deployments of any method. Knocking on doors and directly speaking with residents proved an extremely successful means of bolstering residential placements. However, this method is time-intensive and often requires outreach performed outside of typical business hours. We found speaking at community meetings to be the most efficient means of in-person outreach. Highlighting a locally appropriate flagship species to represent your project may further engender public support and participation (Bowen-Jones and Entwistle 2002). For example, the DC Cat Count is a cat-focused project with neutral messaging (Flockhart et al. In press). As a result, residents who care for outdoor cats, as well as residents who hold negative opinions of outdoor cats, are both particularly interested in participating. It is not uncommon for cooperating partners to express initial interest in the project, but not engage beyond their initial interest. To accommodate this, we recommend identifying and engaging roughly 20% more sampling sites than are needed.

It is in the best interest of all parties involved to receive written permission prior to conducting fieldwork on private property (Dyson et al. 2019). We recommend creating a standard document that contains the cooperating partner's name and address, researchers' name and affiliation, details about the purpose of the project, description of the sampling method, sampling dates, acknowledgment of how the data will be used, and signature line. Legal protection of both the private sampling site and research equipment can also be included in this form and may be required by some entities (e.g. indemnification clauses; 'additional insured' and hold harmless agreements). Due to the varying technological comfortability of the general public, be prepared to email a printable version of this document (i.e. PDF), text or email a digital copy that can be signed without the use of specific applications or programs (e.g. Survey123, Google Forms), or mail a hard copy of the form with return postage. Regardless of the format, it is best practice to digitize and store the responses in the same location and to have them accessible during fieldwork. It is not uncommon for large institutions to maintain their own organization-specific permitting system. If this is the case, it is often easiest to work within the organization's permitting process rather than using the project-specific permission forms. These permits often include space (e.g. comment section) to incorporate specific language from the project-specific permit such as an acknowledgment of how the data will be used, etc.

Depending on the partnering organization, we recommend checking in with the appropriate personnel and presenting these permits upon arrival for fieldwork. Doing so increases transparency and builds a relationship between the landholder and the researcher. In some cases, researchers will be joined by a liaison or resident from the partnering landholder for fieldwork on their property. When accompanied by a liaison, schedule or confirm the date and time of return with the liaison prior to leaving the property to ensure that they will be available, if necessary, to retrieve the cameras. In other cases, such as sampling utility poles, checking in with the governing body after the permits have been obtained is generally not necessary. It is not uncommon for landholders to wish to see the photos taken on their property. When requested, we recommend cooperating when possible, but advice being explicit about what can and cannot be shared (e.g. photos of endangered species, data embargos).

Planning

We recommend keeping a database of potential camera sites that can be used to keep track of the cooperating partners' progress in the paperwork process (e.g. permission form sent, permission form signed). This database should also include the cooperating partners' contact information and specific instructions, such as details on how to enter the property, or conditions for camera placements. While it is appropriate for some of the information contained within the camera site database to be associated with the wildlife observations at that site (e.g. site treatment, geographic coordinates, bait type), information that compromises the privacy of the site owner (e.g. property owner's name, email address) should not be associated with the resulting dataset to ensure the privacy of the cooperating partner. As part of the DC Cat Count, we developed a database using ArcGIS Online and Survey123, a form-based survey application created by Environmental Systems Research Institute. This system uses an online form for potential partners to express interest in hosting a camera and plots their location on an internal map. Field technicians use a similar form when placing a camera to keep track of pertinent metadata, which automatically plots each camera and its status (e.g. deployed, needs review) to the same map. The code for this program, called FELINe (Field Equipment Location and Information Network), can be found in Supporting Document 1. With a limited knowledge of Microsoft Excel, this online application can be adapted to record variables not included in our study but may be needed for other urban camera trapping projects.

Prior to fieldwork, consider creating a fieldwork plan that outlines the sampling areas that will be visited and the contact information for any cooperating partners that may be involved. Site-specific information (access codes for gated properties, etc.) from cooperating partners can also be incorporated here. We have found it especially helpful to include detailed instructions for travel to and between field sites, which can help researchers navigate unfamiliar areas or avoid routes that are temporarily closed due to construction. Researchers may also wish to include listing parking locations, public restrooms, and cooling and warming stations if conducting fieldwork in extreme weather. If using handheld GPS units, it can be helpful to create reference points for each address beforehand and to include these in the field plan. For the safety of those conducting fieldwork, consider sharing your plan with a trusted colleague prior to engaging in fieldwork. This type of plan can be especially helpful to studies that frequently sample new sites. However, not all studies will benefit from this type of planning.

Placements

Considerations when setting cameras in the matrix vary depending on the study objectives. When placing cameras in alleyways or sidewalks, be sure to set the camera out of the human eyeline when possible. Setting cameras low or high off the ground can reduce the chances of passersby noticing and tampering with them. Cameras with a white flash should not be used in areas where people will be driving, as the flash may distract or impair the driver and put them and others at risk. If setting the camera on a utility pole, look for signs of collisions (e.g. rub marks, paint chips) or other indications that the likelihood of a vehicle hitting a camera is high. Avoid placing cameras on utility poles in narrow alleys when possible. In the United States, individuals forego their right to privacy when on public property, as well as when they can be seen on private property from public property. Thus, it is legal to photograph humans in public spaces without the express approval of each individual, unless a local ordinance specifically prohibits it (Wright 2015; Krages 2017). However, to maintain the privacy of passersby, we recommend setting cameras low to the ground to avoid photographing human faces. Researchers should always investigate local ordinances and obtain the proper permits before placing any camera on public property.

When setting cameras on private property, adhere to any conditions given by the landholder. If setting a camera that faces a private home, be cognizant of disturbances caused by white flash. Regardless of flash type, avoid setting cameras that will shoot into windows. Not all yards will present clear paths for wildlife. In these cases, it is best to set the camera near a hole in a fence or shoot across the yard to maximize the chances of documenting wildlife. Some cooperating partners have bait present on their property (e.g. bird feeders, compost piles, cat food). Consider the type and volume of photos you wish to collect if setting cameras around anthropogenic baits. Studies specifically investigating bait site phenomena may benefit from a camera aimed directly at the bait since it is likely that food versus scent lures have varying effects on wildlife detections. For studies not investigating bait site phenomena, we recommend setting cameras that will document animals walking to and from the bait but will not take copious photos of animals at bait. Recording presence of bait at sampling sites is necessary for eventual analyses.

Theft and vandalism can be shockingly low in the urban matrix; in our experience, less than 2% of deployments saw theft or vandalism. This amount is consistent with other urban camera trapping projects (Magle et al. 2019). Of the stolen or damaged cameras, 32% were white flash cameras and remaining 68% were infrared. A higher proportion of infrared cameras displayed evidence of having been hit by vehicles, whereas a higher proportion of white flash cameras displayed evidence of purposeful vandalism. It is best practice to always secure cameras using cable locks and place an asset tag on each camera that includes the project name, investigator and contact information.

Public participation

Public participation in scientific research can be broadly defined as a collaboration between volunteers and scientists to contribute to meaningful research (Cohn 2008; Trimboli and Toomey 2016). While this partnership may be referred to by multiple names (e.g. citizen science), for continuity purposes, we refer to it as 'public participation'. Public participation expands the potential for valuable large-scale data collection, while simultaneously increasing public involvement and interest in the scientific processes and research methods (Brossard et al. 2005; Cohn 2008; Dickinson et al. 2012; Mulligan et al. 2015). We have found public participation to greatly contribute to data collection and photo processing, owing to local knowledge and accessibility to valuable sampling sites.

Engaging with the public, whether it be conversations with passersby regarding our cameras, distributing flyers at community events, or conversing with volunteer camera hosts on their private properties, has provided a mutually beneficial platform for sharing information and fostering community relationships. Members of the public are often eager to share information about the species they have seen in the area, when asked. This information can provide valuable insight into where cameras should be set and aimed. After including residents in the placement process, we have anecdotally found that residents are more likely to express interest in the results of the study. Engaging members of the public and encouraging their input and involvement in research can lead to increased interest, support and knowledge of the scientific processes and ecological questions at hand, particularly if they feel a personal connection to the research in their community (Rovero et al. 2013; Trimboli and Toomey 2016). These interactions, even as isolated incidents, can provide meaningful information for all parties.

The volume of camera deployments and triggers creates an overwhelming backlog of photo processing. Although onboarding and training new volunteers in deploying cameras and processing photos requires staff time and management, it expands the possibilities of large-scale camera trapping efforts, and helps manage the backlog of photos (McShea et al. 2016; Trimboli and Toomey 2016). Time and attention to volunteer training depends on the complexity of the task; but, deploying cameras and processing photos, once sufficiently explained and demonstrated, can be reliably and accurately supplemented by public participation (Cohn 2008; Trimboli and Toomey 2016). McShea et al. (2016) found that properly trained members of the public were able to deploy camera traps correctly 94% of the time and identify species accurately 90% of the time, though accuracy decreased for sympatric congeners. The likelihood of misidentification can be reduced by using a multi-stage verification process. Given that individuals are choosing to volunteer their time, we are careful to assign relatively small deployments, and only increase the frequency or length of their assignments if requested. Photo processing can also utilize public participation via online platforms that allow volunteers to review photographs online (e.g. Zooniverse; Simpson et al. 2014). This approach allows volunteers to assist in photo processing regardless of their physical location or personal schedule, which cannot be overcome as easily when using in-person photo processing during business hours.

We have had success recruiting volunteers through intra-organization volunteer emails, but posting on social media, local list-serves, science volunteer boards or newspapers can also be effective means of outreach. We highly recommend investing time into recruiting, training and managing volunteers in order to collect and process robust data that could not be achieved by staff scientists alone. Public involvement can increase awareness and appreciation of urban wildlife, increase the understanding and importance of research and scientific processes and provide extensive reliable data that can ultimately be published (Brossard et al. 2005; Dickinson et al. 2012; Mulligan et al. 2015).

Processing

Sampling in the urban matrix poses the daunting task of sorting through thousands of photos triggered by humans and vehicles. Although this high volume of photos, particularly in alleys, sidewalks and walking trails, is equally undesirable and inevitable, it is necessary for successful and representative sampling. Careful thought on specific deployments within these areas can help manage this to a degree. We recommend a review of available photo-processing software to assess its ability to provide important data variables and program capabilities that are identified for a specific project. Ivan and Newkirk (2016) and Young et al. (2018) published reviews of 7 and 12 known photo-processing programs, respectively, that were assessed against a range of characteristics and data variables. Due to a lack of standardized data management software, many programs are developed to meet their own specific project requirements, and have varying capabilities tailored for those projects (Forrester et al. 2016; Thomson et al. 2018). Moving forward, it will be advantageous to create a standardized software management program that can meet the diverse requirements for all camera-trapping efforts in order to allow consistent collaboration and comparison among projects (Forrester et al. 2016; Young et al. 2018). Members of the public can assist with photo tagging and will greatly contribute to the efficiency of photo-processing and reduce the backlog of data. Due to the volume of photos being manually sorted, we emphasize the importance of having multiple review steps to ensure data accuracy.

There have been multiple attempts, with mixed success, to develop automatic species recognition processes (Yu et al. 2013; Swinnen et al. 2014; McShea et al. 2016; Norouzzadeh et al. 2018). Norouzzadeh et al. (2018) proposed that deep neural networks can save a large percentage of human time and labor by automatically identifying empty images versus images with animals, accepting information from images that the deep learning network has high confidence in, and providing humans with a 'top five' list of suggestions of species to choose from. Although fully automating the task of tagging photos is not currently a reliable or feasible option, artificial intelligence can potentially assist in photo-tagging by recognizing and discarding certain photos at high confidence levels (misfires, humans, vehicles) and allow for more efficient photo-processing (Swinnen et al. 2014; McShea et al. 2016; Norouzzadeh et al. 2018). A critical analysis of this approach may be warranted, as this could result in the loss of data pertaining to the presence of factors that may help explain animal occupancy and behavior (e.g. humans and vehicles). Regardless, as artificial intelligence continues to develop, the reduction of photos that are currently present in such high volume may allow sampling in the urban matrix to become a less daunting task.

While the challenges presented by urban field work can seem intimidating, we have found that the *Five P's of urban ecology* can provide a targeted and intentional approach to fieldwork. Through the DC Cat Count, a city-wide effort to estimate the outdoor cat population in Washington, DC (Flockhart et al. In press), we have deployed camera traps at over 1000 urban locations—most of which occur within the urban matrix. To demonstrate the importance of sampling beyond large urban green spaces to understanding the complexities of urban ecosystems, we used occupancy models to examine the differences in the distributions of eight representative mammals of urban ecosystems, across the urban matrix and green space gradient, while accounting for imperfect detection (MacKenzie et al. 2017).

Materials and methods

Case study: the DC Cat Count

The DC Cat Count is a 3-year collaborative study aiming to estimate the total cat population in Washington, DC including indoor, shelter and outdoor cat populations and to understand the movement of cats among these populations via human interventions such as adoption and abandonment (Flockhart et al. In press). Camera-trapping is the primary survey method for estimating the free-ranging cat population and will subsequently help inform data-driven population management and points of effective intervention. To illustrate how the *Five P's of urban ecology* facilitated our sampling effort, we have stratified the methods by each principle and describe planning before partnerships for the benefit of the reader.

Planning

We used land cover and US census data to stratify Washington, DC into 400×400 m cells and categorized each cell by its

Table 1: Proportions of sampling cells and sampling efforts across the 2018 and 2019 sampling seasons.

Sampling cell type	Prevalence of cell type in city	Proportion of cell type sampled	Number of deployments in each cell type	Proportion of cameras stolen/ vandalized in cell type
Low income × undeveloped	0.78%	0.00%	0	0.00%
Low income × intermediate development	15.5%	2.63%	30	0.00%
Low income × high development	6.2%	5.26%	67	0.00%
Medium income × undeveloped	8.53%	10.53%	105	0.19%
Medium income × intermediate development	29.46%	28.85%	331	0.28%
Medium income × high development	15.50%	26.32%	288	0.85%
High income × undeveloped	13.95%	21.05%	181	0.00%
High income × intermediate development	9.30%	5.26%	57	0.00%
High income × high development	0.78%	0.00%	0	0.00%

Discrepancy between cell type abundance and sampling efforts were addressed in the 2020 sampling season, but data were not included in current analyses.

predominant degree of urbanization (high development, intermediate development, undeveloped/open) and predominant relative household income (low income, medium income, high income) based on data from the National Landcover Database and US Census Bureau. We further examined patterns of reported incidents of violent crime over the previous year using a hotspot analysis (ArcMap 10.8; Scott and Warmerdam 2005). Thirteen sampling cells contained violent crime density statistically above (99% confidence interval) the rest of Washington and were excluded from our project. Due to limited time and equipment, only a subset ($n = 212$) of sampling cells were surveyed throughout the project. Surveyed sampling cells were selected in approximate proportion to their abundance in the city (Table 1).

Partnerships

Access to privately-owned sites was primarily solicited via social media and cold calls, which accounted for 62% and 22% of residential deployments, respectively. Newsletters, community meetings, and canvassing comprised the remaining 16% of deployment sites. We found that landholders returned signed paperwork roughly 84% of the time, albeit many residents had to be reminded several times before returning paperwork to allow property access. Sites were not used without the written permission of the appropriate party.

Placements

Within designated sampling cells, we deployed a combination of infrared-flash and white-flash camera traps (Reconyx HyperFire 2, Reconyx Inc., 3828 Creekside Ln, Ste 2, Holmen, WI 54636) 0.2–0.5 m off the ground, aimed perpendicular to a likely animal pathway (e.g. dirt pathway, alley, along a fence line) such that the flanks of detected animals would be photographed for individual identification. Cameras captured five consecutive photographs upon each trigger with no delay. Multiple photographs of the same individual(s) taken in immediate succession (<1 minute apart) were considered single detections. We rotated cameras through sampling cells and deployed cameras for 15 days at a given site, with each deployment consisting of a single camera. We surveyed sampling cells from September to December 2018 and April 2019 to January 2020. Camera density across sampling cells varied depending on public participation and viable placement options, with as few as 10 cameras/km^2 and as many as 75 cameras/km^2. We avoided the use of any scent or food lure but documented when a resident regularly left cat food near the camera site.

Public participation

Cooperating partners were reminded of their participation via email or phone call approximately 1 week prior to our arrival. Residents were assured that they did not need to be present but were invited to participate in the camera deployment if desired. Specific instructions or requests from residents were primarily received in response to this outreach. Volunteers aiding in photo processing were recruited via emails to existing volunteer networks at both the Humane Rescue Alliance and the Smithsonian Conservation Biology Institute.

Processing

We uploaded all photos into eMammal, a camera-trap data management system and photo repository developed by the Smithsonian Institution (Zhao and McShea 2018, see also http://emammal.si.edu). The eMammal platform provides software to automatically import photos and associated standard metadata, with efficient means of viewing, tagging, and uploading photos, multi-step review process to ensure data quality and maximum accuracy, automatic archival of approved data, and public access for viewing and analyzing data (McShea et al. 2016; Young et al. 2018). Following photo review, we created daily detection histories for each camera trap site for eight urban mammals using the CamtrapR package (Niedballa et al. 2016) in program R: eastern chipmunk (*Tamias striatus*), eastern cottontail (*Sylvilagus floridanus*), eastern gray squirrel (*Sciurus carolinensis*), white-tailed deer (*Odocoileus virginiana*), Virginia opossum (*Didelphis virginiana*), northern raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*) and brown rat (*Rattus norvegicus*). Domestic cat and dog (*Canis familiaris*) were also regularly detected but were not included in this analysis due to data sensitivity and direct association with humans (i.e. leashed dogs), respectively. Other species such as coyote (*Canis latrans*), bobcat (*Lynx rufus*), North American river otter (*Lontra canadensis*), muskrat (*Ondatra zibethicus*), southern flying squirrel (*Glaucomys volans*), white-footed mouse (*Peromyscus leucopus*), house mouse

(*Mus musculus*) and North American beaver (*Castor canadensis*) were detected, but the resulting data were too sparse for analyses.

Landscape variable and occupancy models

Cameras were assigned to either the warm (April–August) or cold (September–January) season, based on their deployment dates. For occupancy analyses, the urban landscape was further classified into land cover and land use. Based on Sanwick et al. (2003), we used gray space, semi-natural green space and functional/amenity green space to describe land cover at a site. Functional and amenity green spaces were defined as green space that regularly received maintenance (e.g. landscaping) or are otherwise not semi-natural and were considered regardless of property ownership. To assess land use, we continued to use gray space and semi-natural green space, but categorized sites in functional and amenity green spaces into yards or parks according to their ownership. Development density was categorized to reflect low, intermediate and high levels of development (undeveloped, low/medium development and high development) based on the National Landcover Database classification that occupied the greatest proportion of the site's sampling cell (Wickham et al. 2014). We compared 11 *a priori* models to predict the occupancy for each of the eight mammal species while explicitly estimating the daily probability of detection due to the elusive and cryptic nature of urban mammals. These models were hierarchical and included a null model in which covariates were not considered for the probability of site occupancy (Ψ, e.g., site use) or probability of detection (p; [Ψ(.),p(.)]), as well as a model in which seasonality was considered for p, but not Ψ since none of the species observed are known to hibernate. The seasonality-only model consistently provided greater support than the null model, so all remaining models considered seasonality on p, and each covariate on either Ψ, p, or both Ψ and p. We ranked models based on their AICc weights and drew our inferences from top-supported models and considered habitat associations to be strong if the 95% confidence intervals did not overlap each other (Burnham and Anderson 2002). All occupancy models were developed in the 'unmarked' package (Fiske and Chandler 2011).

Results

We deployed 1059 cameras in 148 sampling cells throughout Washington, DC over two field seasons (2018–2019). The survey effort resulted in 264 942 observations of 32 species detected over 13 132 trapdays. Fifty-three percent of these cameras were placed in urban green spaces, while the remaining 47% of placements were in the urban matrix. Sixty-eight percent of cameras were placed on public property (parks, forests, alleys, sidewalks), while the remaining 32% were placed on private property (front yards, side yards, back yards, driveways, etc.).

We used data from 938 deployments in the occupancy analyses due to camera malfunctions, theft, or inadequate site metadata (e.g. insufficient reporting of predominant groundcover). Humans, false-triggers, and vehicles accounted for 30%, 21% and 15% of all camera detections, respectively. The remaining detections were primarily mammals (26%) and birds (6%). Of the mammals detected, 55% of observations were native wildlife and 35% were of non-native species including brown rats, house mice and domestic cats and dogs. The remaining 10% ($\sim$3% of total observations) were not identifiable to species (e.g. unknown rodent species).

Occupancy of most species was associated with the degree of development in its sampling cell (Table 2). However, raccoons, white-tailed deer and eastern chipmunks were more strongly influenced by land use (Fig. 3). Most species were positively associated with undeveloped or semi-natural land. Species' association with semi-natural habitats was apparent based on the occupancy probabilities for raccoons (Ψ = 0.87 $\pm$ 0.02 SE), white-tailed deer (Ψ = 0.82 $\pm$ 0.02 SE), eastern gray squirrel (Ψ = 0.93 $\pm$ 0.02 SE) and red fox (Ψ = 0.78 $\pm$ 0.03 SE). Despite low detections, this pattern was also apparent for eastern chipmunks (Ψ = 0.19 $\pm$ 0.02 SE). White-tailed deer and red foxes exhibited pronounced differences in their occupancy of the remaining urban landscape, with deer showing a stronger association with parks (Ψ = 0.23 $\pm$ 0.04 SE) than yards and gray space, and foxes exhibiting a stronger association with intermediate development (Ψ = 0.30 $\pm$ 0.03 SE) over high development (Ψ = 0.04 $\pm$ 0.01 SE). The top model for eastern cottontails yielded a nonsensical estimate, so we derived inferences from the second ranking model that assumed constant occupancy across sites (Ψ = 0.13 $\pm$ 0.02 SE).

Brown rats and Virginia opossums did not exhibit the highest occupancy in undeveloped areas. Virginia opossums were most strongly associated with intermediate development (Ψ = 0.38 $\pm$ 0.03 SE), though this association was not notably different from that of undeveloped areas (Ψ = 0.35 $\pm$ 0.07 SE). Brown rats were the only species to be most strongly associated with high development (Ψ = 0.50 $\pm$ 0.04 SE). Predictably, brown rat occupancy fell in intermediate development (Ψ = 0.44 $\pm$ 0.03 SE) and undeveloped areas (Ψ = 0.01 $\pm$ 0.01 SE).

Daily detection probability was similar between the warm and cold seasons. However, since the majority of our sampling occurs in the warm season, we report only the warm season daily detection probabilities herein. Daily detection probability was highest in semi-natural or undeveloped areas for raccoons (P = 0.47 $\pm$ 0.01 SE), white-tailed deer (P = 0.30 $\pm$ 0.01 SE) and eastern gray squirrels (P = 0.48 $\pm$ 0.01 SE) compared to other land covers, and highest in parks for eastern chipmunks (P = 0.69 $\pm$ 0.06 SE). The lowest detection probabilities for Virginia opossums was in undeveloped areas (P = 0.09 $\pm$ 0.01 SE), whereas lowest detection probabilities for eastern cottontails was in areas with high development (P = 0.001 $\pm$ 0.001 SE). These exceptions aside, detection probability was relatively constant across habitat covariates for all species (Fig. 3).

Discussion

Mammals varied in their use of the urban landscape, corresponding with previous research (Cove et al. 2019; Moll et al. 2020). For this analysis, we broadly defined green space as any land predominantly covered in vegetation. We further stratified green space by land use (semi-natural, park and yard) and land cover (semi-natural and landscaped). In general, many of the species display a strong habitat association with semi-natural areas, reinforcing their role as habitat patches and emphasizing the importance of the conservation and sampling of this type of urban green space. However, use of the remainder of the matrix varied by species. For instance, raccoon and white-tailed deer site use was strongly associated with semi-natural areas, but deer exhibited higher site use of parks than in yards or the developed environment, whereas raccoons used these sites interchangeably. Eastern gray squirrels were also more strongly associated with semi-natural areas but remained common across the remainder of the urban matrix.

Table 2: Information distances from the top-ranking models based on Akaike Information Criterion (Δ AIC) for urban mammals across all models compared in occupancy [Ψ] (*covariate*), detection probability [P] (covariate) notation.

Species (n observations)	Δ AIC: Ψ(), P(season)	Δ AIC: Ψ(land use), P(season)	Δ AIC: Ψ(),P(season + land use)	Δ AIC: Ψ(land use), P(season + land use)	Δ AIC: Ψ(land cover), P(season)	Δ AIC: Ψ(), P(season + land cover)	Δ AIC: Ψ (land type), P(season + land cover)	Δ AIC: Ψ(development), P(season)	Δ AIC: Ψ(),P(season + development)	Δ AIC: Ψ(development), P(season + development)
Raccoon (6210)	387.09	138.92	229.14	0.00*	138.00	239.14	8.84	142.45	314.15	97.41
White-tailed Deer (5999)	526.40	71.45	327.03	0.00*	82.05	353.76	8.59	112.55	258.02	98.77
Eastern Chipmunk (800)	103.29	55.48	37.26	0.00*	54.08	76.84	37.63	39.64	101.81	37.30
Eastern Gray Squirrel (25 009)	339.91	273.29	112.13	48.94	271.92	110.70	46.12	271.36	66.82	0.00*
Red Fox (1971)	354.38	110.73	311.13	100.24	125.02	326.82	115.92	0.96	214.41	0.00*
Virginia Opossum (1896)	95.48	90.03	80.07	81.20	88.40	82.07	81.34	47.67	35.76	0.00*
Eastern Cottontail (726)	94.55	98.89	87.37	91.55	97.04	86.72	89.06	37.59	5.25	0.00*
Brown Rat (7729)	199.47	124.16	103.55	73.69	122.46	123.69	91.55	9.72	153.17	0.00*

The top-ranking model for each species is denoted by an asterisk.

Two species maintained different habitat associations and displayed high site use of developed areas. Brown rat site use was best predicted by the greatest levels of development density, which are typically the most under-sampled and challenging areas to survey. Thus, rodent management efforts are rarely research-based, and rodent control could be largely ineffective due to lack of ecological understanding of urban rats (Parsons et al. 2017). More surprisingly, Virginia opossums showed a higher site use of areas with intermediate development over semi-natural areas. This may be due to the strong association between urban opossums and proximity to water, which is likely greater in low-density residential areas due to open gray infrastructure, irrigation, etc. (Fidino et al. 2016; Wait and Ahlers 2020). Exclusive sampling of semi-natural areas may yield artificially low projections of urban opossum and rat distributions, if results are extrapolated beyond the areas sampled. Accurately assessing these populations is especially critical for public health, considering the emphasis placed on rats as carriers of zoonotic diseases (Strand and Lundkvist 2019; Dahmana et al. 2020; Murray et al. 2020), and opossums as a natural means of tick-borne illness mitigation (Keesing et al. 2006, 2009; Ogden and Tsao 2009).

For most species included in this analysis, the relatively low occupancy probabilities in non-natural habitat make it appealing to dismiss sampling the urban matrix. However, the present occupancy probabilities in the urban matrix are comparable to occupancy estimates from other surveys of natural habitats. The estimated occupancy of eastern gray squirrels reported herein the urban matrix (intermediate development: $\Psi = 0.77 \pm 0.02$ SE; high development: 0.64 ± 0.03 SE) is higher than the estimated occupancy from forested conservation areas in Missouri ($\Psi \approx 0.57$) or Illinois ($\Psi \approx 0.20$; Pease et al. 2019; Kays et al. 2020b, respectively). Similarly, urban matrix occupancy of red foxes (intermediate development: $\Psi = 0.30 \pm 0.03$) in Washington, DC is roughly equal to red fox occupancy in a landscape of state-managed natural areas in southern Illinois ($\Psi = 0.26 \pm 0.04$ SE) or along the central portion of the Appalachian Trail Corridor in ($\Psi \approx 0.24$; Erb et al 2012; Lesmeister et al. 2015). We draw attention to these comparisons to illustrate that the urban matrix is not void of wildlife, but actually comparable in site use across species in non-urban settings. Non-biased sampling of habitat within urban landscapes allows for more well-informed ecological research, a greater understanding of abundance and overlap of wildlife within the urban matrix, and, ultimately, more effective urban planning. Representative sampling within urban environments will become increasingly more important as further development and habitat fragmentation make natural, undisturbed habitat scarcer and less connected.

Despite the importance of non-biased sampling, the logistic constraints imposed by sampling urbanized areas are daunting to many ecologists (Dyson et al. 2019). Through the DC Cat Count, we have demonstrated that these barriers can be overcome through the thoughtful adherence to the *Five P's of urban ecology*. Careful consideration for each of these principles resulted in a robust sampling effort of habitats roughly proportional to the landcover present in Washington, DC, and the continued processing of our data despite the large quantity of photos collected. In addition to the value provided to the present study, this sampling strategy has yielded data that have contributed to our understanding of urban food webs, as well as our understanding of national trends in wildlife—further supporting the applicability of this type of sampling for a wide range of research questions (Cove et al. In press; Herrera and Cove 2020).

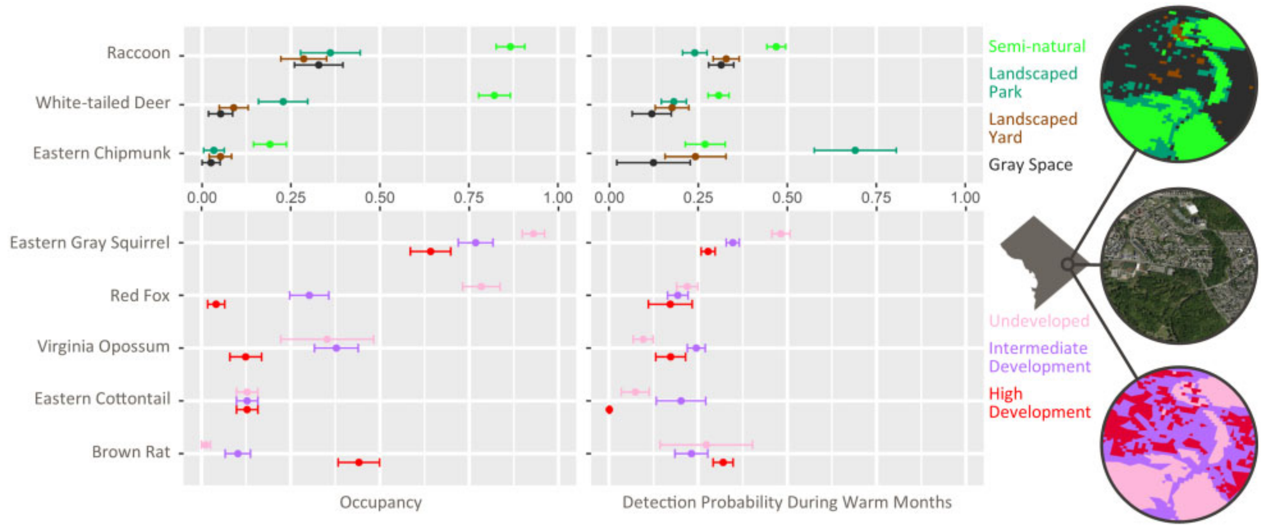

Figure 3. Estimated occupancy, detection probability and associated 95% confidence intervals plotted from each species' top-ranking model. Maps of the same sampling area depicting land use (top) and development (bottom) are also included for illustrative purposes. Land use was recorded in situ when each camera was deployed. Each site was assigned a level of development based on the predominant degree of development within 400 × 400 m sampling cells.

Conclusions

Urban mammal occupancy varies across the landscape but is not restricted to natural landcover. Indeed, most native mammal species using intact urban green spaces also use other more abundant landcovers in the urban matrix. Here, we show that semi-natural areas in the urban environment are critical, but we also suggest researchers elevate the rest of the city to be viewed as potential habitat and corridors. Our analyses illustrate the importance of the entire urban landscape to many species, as well as the need to include the entire urban matrix in urban ecology research. We acknowledge that conducting research in the urban matrix presents barriers uncommon in other study systems. To help overcome these barriers, we developed the *Five P's of Urban Ecology* to provide researchers with an approach to overcome concerns about working in the urban matrix, enabling sampling across the entirety of the urban landscape and contributing to a greater understanding of urban ecology—an insight greatly needed in a rapidly urbanizing world.

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Authors' contributions

Michael Cove, William McShea, and Tyler Flockhart designed the methodology; Daniel Herrera and Michael Cove collected the data; Daniel Herrera led the analysis and writing of the manuscript with significant contributions from Sophie Moore and Michael Cove.

Conflict of interest statement. None declared.

Data availability

Data will be made available via eMammal (www.emammal.si.edu; project name: D.C. Wildlife Project) in December, 2023 following embargo.

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